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Defining a clade by morphological, molecular, and toxinological criteria: distinctive forms related to *Conus praecellens* A. Adams, 1854 (Gastropoda: Conidae)[†]

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ABSTRACT

We carried out a definition of the *Conus praecellens* A. Adams, 1854, species group using a combination of comparative morphological data, molecular phylogeny based on standard genetic markers, and toxinological markers. Prior to this work, *Conus praecellens* was generally postulated to belong to a clade of similarly high-spired, smaller species such as *Conus pagodus* Kiener, 1845, *Conus memiae* (Habe and Kosuge, 1970) and *Conus arcuatus* Broderip and Sowerby, 1829. The molecular phylogeny and toxinological data demonstrate that these earlier hypotheses are incorrect, and that instead, *Conus praecellens* is in a branch of *Conus* that includes *Conus stupa* (Kuroda, 1956), *Conus stupella* (Kuroda, 1956), *Conus acutangulus* Lamarck, 1810, and surprisingly, some species that are morphologically strikingly different, *Conus mitratus* Sowerby, 1870, and *Conus cylindraceus* Broderip and Sowerby, 1830. A more careful analysis of the morphologically diverse forms assigned to *Conus praecellens* suggests that from the Philippine material alone, there are at least three additional species new to science, *Conus andremenezi*, *Conus miniexcelsus*, and *Conus rizali*. A reevaluation of protoconch/early teleoconch morphology also strongly suggests that *Conus excelsus* Sowerby III, 1908, is related to these species. Together, the different data suggest a clade including the 10 species above that we designate the *Turriconus* (Shikama and Habe, 1968) clade; there are additional distinctive forms within the clade that may be separable at the species level. The phylogenetic definition using the multidisciplinary approach described herein provides a framework for comprehensively investigating biodiverse lineages of animals, such as the cone snails.

Additional keywords: Neogastropoda, *Turriconus*, 12SrRNA sequences, phylogenetic analysis, exogenes

INTRODUCTION

The evolutionary histories of biodiverse *Conus* lineages are a challenge to elucidate. In part this is because the genus is so speciose (about 700 species) but also because most prior data in the literature is morphological. The usual approach is to characterize each species in the lineage based on its shell morphology and to evaluate phylogenetic relationships using additional anatomical data, when available.

Prior attempts to divide *Conus* into subgeneric groups have been based largely on shell morphology. In this work, we focus on one particular branch of *Conus* that includes the species known as *Conus praecellens*. Several previous attempts to determine which species are most closely related to *Conus praecellens* have grouped *C. praecellens* with other high-spired forms (Figure 1) that are collected in deep offshore locations. Some of the specific prior hypotheses that have been proposed are summarized in Table 1.

In the most comprehensive modern treatise on Indo-Pacific *Conus* species (Röckel et al., 1995), *Conus praecellens* is regarded as most closely related to *Conus acutangulus*. In most of the schemes shown in Table 1 (Marsh and Rippingale, 1964; Okutani, 2000), *Conus praecellens* is grouped together with *Conus acutangulus* in the subgenus *Conasprella* Thiele, 1929. The designated type of *Conasprella* is "*C. cancellatus*" (= *C. pagodus*). Another species generally thought to belong to this subgenus is the Eastern Pacific *Conus arcuatus*. In one of the proposals (da Motta, 1991), *Conus praecellens* and *Conus acutangulus* are in two different subgeneric groups: *Conus praecellens* in *Conasprella* and *Conus acutangulus* in *Kermasprella* Powell, 1958 (which this author regards as a subgenus of the genus *Profundiconus* Kuroda, 1956). Among the species included with *Conus acutangulus* in *Kermasprella* are forms such as *Conus memiae* and *Conus ncreis* (Petuch, 1979), the latter regarded by Röekel et al., 1995 as a form of *Conus wakayamaensis* (Kuroda, 1956). Thus, the high-spired

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Figure 1. High-spired *Conus* species previously postulated to be related to *Conus praecellens*: Top from left: *Conus acutangulus*, "typical form"; *Conus acutangulus*, "deep-water form"; *Conus nereis*. Middle from left: *Conus praecellens*, "Aliguay form"; *Conus praecellens*, "sowerbii form"; *Conus andremenezi* new species (Holotype, MSI); *Conus pagodus*. Bottom from left: *Conus miniexcelsus*, new species (Holotype, deposited at MSI); *Conus rizali* new species (Paratype 2, MSI); *Conus arcuatus*. All of the specimens shown are from the Philippines, except for *Conus arcuatus*. Measurements provided in Appendix 1.

Table 1. Previous taxonomic assignments of *Conus praecellens* and *Conus acutangulus*.

Marsh and Rippingale (1964):	DaMotta (1991):	Okutani (2000):
Conasprella praecellens pagodus arcuatus acutangulus wakayamaensis	*Conasprella praecellens pagodus arcuatus*	*Conasprella praecellens pagodu gracatapi acutangulus*
	Kermasprella acutangulus memiae wakayamaensis nereis jaspideus	*Endemnoconus memiae wakayamaensis ione*

Conus species including *Conus praecellens* were either all grouped together in *Conasprella*, or were divided into a *praecellens/pagodus* group (*Conasprella*) and an *acutangulus/memiae* group (*Kermasprella*).

These shell morphology-based suggestions can be independently evaluated using molecular data. If only morphologieal analyses are used, the resulting systematics may not reflect evolutionary trends as the traits may be subject to selection forces that do not reflect common descent. Distinguishing similarity by descent (reflecting the phylogeny) from similarity directed by selection (convergence or parallelism) is problematie without independent data corroborating the morphologieal evidence. Hence a widespread attempt to define biodiversity using molecular markers, notably a segment of the COI gene, has led to the "barcode initiative". Although this initiative has been widely implemented, workers who need to identify field speeimens require a more seamless integration of the molecular with the morphologieal data.

Our first goal is to define a phylogenetic tree with clades that reflect the branching pattern and in turn the evolutionary history of the species. Moleeular data provide independent evidence for such a phylogeny and a useful organizational framework for in-depth studies of species-rich groups. The morphological traits mapped onto such a tree distinguish the respective roles of common descent and selection in the evolutionary process.

In this work, we focus on the definition of the putative clade that includes *Conus praecellens*. Using 12SrRNA sequences, we speeifically evaluate which *Conus* species are most closely related to *Conus praecellens*. In addition to using a molecular phylogeny to assess morphology-based taxonomy, we have gathered molecular data in the form of the genes that encode toxins expressed in the venom ducts of cone snails. As will be shown, these highly specialized "exogenes" (Olivera, 2006) are useful in defining diserete branches of a large biodiverse lineage such as the cone snails. This three-pronged approach defines a more complete picture of the evolutionary history of these biodiverse cone snails with the result that previous morphologically informed hypotheses may be more objectively assessed.

MATERIALS AND METHODS

Specimen Collection. Most forms in the *Conus praecellens* complex are collected offshore from 30–250 meters in depth. The bulk of Philippine specimens in collections assigned to this species were collected (together with such species as *Tibia fusus* (Linnaeus, 1758) and *Xenophora solaris* (Kosuge and Nomoto, 1972) around 1960, primarily from a few classical fish trawler loealities (Maqueda Bay in Samar Is, Tayabas Bay in Luzon); at the time, these were mostly identified as *Conus souverbii* (see Reeve, 1849; Springsteen and Loebrera, 1986). Because other forms in the *praecellens* complex are mostly from even deeper water, these were less well represented in collections; most specimens available in museums are poorly preserved and/or dead-collected. However, the combination of gill net and hookah collections in the Cebu/Bohol area of the Central Philippines and intensive small trawl collections around the Island of Aliguay has increased accessibility to several forms in the *Conus praecellens* complex. Some of these are smaller specimens that were sparsely represented in earlier collections. A range of live-collected specimens with preserved protoconchs has become available, which has facilitated the reevaluation of the *Conus praecellens* species complex.

Phylogenetic Analysis. We aligned sequences using Clustal X (Larkin et al., 2007) and refined by eye using MacClade (Maddison and Maddison, 2005). The tree was inferred using MrBayes (Huelsenbeck et al., 2001; Ronquist and Huelsenbeck, 2003). The run comprised 1,000,000 generations with the first 25% of the sampled generations discarded as burn-in trees. Two MCMCMC runs (metropolis-coupled Monte-Carlo markov-chain), using four chains each, were used to thoronghly explore tree space. Convergence of the likelihoods was determined by comparing the average standard error of the differenee (ASED) in split frequencies between the two runs and by comparing plots of the log-likelihood after the burnin to the end of the runs. Optimality was also judged adequate when the PSRF (Potential scale reduction factor) for the total tree length and for each model parameter reached 1.00.

Identification and Sequencing of Genomic Clones Encoding O-Superfamily Peptides. Genomic DNA was prepared from 50 mg each of tissues of *Conus acutangulus*, *Conus mitratus*, *Conus praecellens*, and *Conus stupa* using the Gentra PUREGENE DNA Isolation Kit Kit (Gentra Systems, Minneapolis, MN) according to the manufacturer's standard protocol. These genomic DNAs were used as templates for polymerase chain reaction (PCR) with oligonucleotides corresponding to conserved 5′ intron and 3′ UTR sequences of omega and delta prepropeptides. The resulting PCR products were purified using the High Pure PCR Product Purification Kit (Roche Diagnostics, Indianapolis, Indiana) following the manufacturer's suggested protocol.

The eluted DNA fragments were annealed to pNEB206A vector and the resulting products transformed into competent DH5a cells, using the USER Friendly Cloning Kit (New England BioLabs, Beverly, Massachusetts) following manufacturer's suggested protocol. The nucleic acid sequences of the resulting omega and delta toxin-encoding clones were determined according to the standard protocol for automated sequencing.

Morphometric Analysis. Using dial calipers, we measured maximum diameter (mm) and total length (mm; including spire height) of species within the *praecellens* complex. Relative diameter was calculated as the ratio of maximum diameter to total length. All species were represented by multiple samples. In view of the low between-sample variation, we calculated a single mean relative diameter for each species.

RESULTS

Systematic Descriptions of Three New Species of *Conus*
by Baldomero M. Olivera and Jason Biggs

Superfamily Conoidea Fleming, 1822
Family Conidae Fleming, 1822
Subfamily Coninae Rafinesque, 1815
Genus *Conus* Linnaeus, 1758

Conus andremenezi Olivera and Biggs, new species.
(Figures 1, 2, 6)

Description: Biconical in shape, mature specimens from 25–53mm. Moderately solid, and with a relatively high spire, and generally broader than most related forms (D/L $\approx$ 0.47). Last whorl is broadly conical, with raised spiral ribs that are not smooth but always undulating (and in some specimens, the ribs seem to have arch-like protuberances, instead of a continuous smooth rib). Raised ribs on the body whorl are well separated from each other, with interstices that have axial scales between them.

The body whorl has an off-white ground color with characteristic purplish-brown spots that occur in zones; in the two darker zones, the spots generally cover more spiral ribs and extend into the interspaces (although there is considerable variation). The protoconch is decollated in most specimens, but when preserved it is a rounded conical shape, translucent, very light yellowish brown or off-white; the protoconch is followed by two white early teleoconch whorls that are lightly nodulose and angled at the periphery. The spots begin to appear on the periphery of the third or fourth teleoconch whorl, and typically these are more closely spaced to each other than are the larger spots in the later spire whorls.

Type Material: The Holotype is deposited in the Marine Science Institute (MSI) at the University of the Philippines; Paratypes are deposited at the Academy of Natural Sciences of Philadelphia, Philadelphia, Pennsylvania (ANSP 421619); the Muséum national d'Histoire naturelle, Paris, France (MNHN 21131); the Field Museum of Chicago, Chicago (FMHN 312461); the Harvard Museum of Comparative Zoology, Cambridge Mass (MCZ 361611); Zoological Museum of Moscow State University, Moscow, Russia (Le-37964) and The Bailey–Matthews Museum, Sanibel, Florida (BMSM 38672) (see Appendix or a complete listing of paratypes).

Type Locality: The type locality for *Conus andremenezi* is Aliguay Island, Philippines, where most specimens in the type series have been collected by commercial fishermen using small trawls at depths around 150 m. Another established locality is off Panglao, Bohol, from Balicasag Island to Momo Beach where the species has been collected by tangle nets in deeper water (~200–300m).

Geographical Distribution: From the Central to Northern Philippines, probably to Viet Nam and possibly much further West (see discussion below). In the recent book of Thach (2005), the specimen figured as *Conus praecellens* (Plate 61, Fig. 34) is likely to be a specimen of *Conus andremenezi*.

Etymology: This species honors the memory of Andre Menez, one of the giants of the field of toxinology.

Remarks: The sculpture on the spire whorls is diagnostic: the spiral ribbons on the larger spire whorls are raised, relatively narrow to very narrow, and always far apart. The wide spacing on the spire whorls between narrow raised spiral ribs is a diagnostic trait of this species; in most similar forms, the spiral ribbons or ridges are much closer together and are more like flattened ribbons, broad and shallow. The broad shape, purplish-brown spots, undulating spiral ribs, and widely spaced ribs on the spire are characteristic features that separate the species from similar forms.

When the protoconch is decollated, this species is difficult to separate from some closely related forms that are potentially variants of *Conus praecellens*. Most specimens can generally be differentiated by the distinctive purple-brown color, the broader shell, the widely spaced spiral ribbons on the spire whorls, and when preserved, the conical protoconch. Most specimens in the type series come from Aliguay.

There is a group of Philippine specimens, not from the type locality, which we tentatively assign to this species. These were collected by the Musorstom expeditions promoted by the Muséum national d'Histoire naturelle, Paris, to Lubang Island/Mindoro. Several large mature specimens of *Conus andremenezi*, all dead collected, were examined. All of these were collected at depths between 160–198 meters; at more shallow collection stations, this form was absent and a narrower *Conus praecellens* variety was present. This provides a more accurate estimate of the depth at which this species occurs.

Finally, there is a small specimen figured by Röckel et al. (Plate 54, Fig. 14) that appears to be a juvenile of *Conus andremenezi*; if the identity of this specimen can

Figure 2. Two morphospecies with non-"*praecellens*-like" protoconchs from Aliguay. All of the specimens shown are from Aliguay Island, Philippines, except the lower left specimen which was collected from southern Japan. Top row: *Conus andremenezi*; Bottom row: *Conus miniexcelsus*. For *Conus andremenezi*, the Holotype (left), Paratype 7 (second from right), and Paratype 11 (right) are shown. For *Conus miniexcelsus*, the Holotype (second from right), Paratype 2 (third from right), and Paratype 18 (rightmost specimen) are shown. All of the types figured are deposited at the Marine Science Institute (MSI), University of the Philippines. Measurements provided in Appendix 1.

be verified, it extends the range of this species across the entire Indian Oeean since the speeimen is reported to be from Somalia. Thus, although almost all of specimens examined were from the Central Philippines, there is strong evidence for the occurrence of the speeies in the Northern Philippines, and the possibility that it may have a geographie distribution that is much wider is raised by the Somali specimen in the Raybaudi-Massila eollection.

Conus miniexcelsus Olivera and Biggs, new species
(Figures 1, 2, 4, 6 and 8)

Conus praecellens f. subaequalis.—Robin, 2008: 424, fig. 14 (non *Conus subaequalis*, Sowerby III, 1870)

Description: A moderately small shell; adult size range, 25–37 mm. High-spired, with both spire and body whorl

having a straight outline, making the shell narrowly biconical. The larval shell has 3.0–3.5 whorls, translucent brownish or purplish. There are 9–11 teleoconch whorls, the first three being ivory-white, without spots, providing a notable contrast to the translucent-colored protoconch. At around the fourth teleoconch whorl, broad brownish spots appear, centered around the periphery. The ground color is white, with chestnut-brown spots. On the body whorl there are a series of flat spiral ribbons. The shell pattern on the body whorl can be divided into 3–5 zones. The most posterior, next to the suture, are a series of about 6 spiral ribbons with extremely fine chestnut brown spots. These are followed by a zone with 3 noticeably broader spiral ribbons that have deeper brown and larger spots. In most specimens, this is followed by three spiral ribbons that have a finer spotted pattern (but not as fine as in the spiral ribbons in the first zone, closest to the suture). The remainder of the shell towards the tip is covered by spiral ribbons that are darker in color and more heavily spotted; typically the first 3 to 4 are darker than those towards the anterior end of the shell, although there is considerable variation in this regard. In some specimens, the light zone continues to the anterior of the shell.

Type Material: The Holotype is deposited at the Marine Science Institute at the University of the Philippines, Paratypes are deposited at the Field Museum, Chicago, Illinois (FMNH 312462); the Museum National d'Histoire Naturelle, Paris, France (MNHN 21132); the Harvard Museum of Comparative Zoology, Cambridge, Massachusetts (MCZ 361609); the Academy of Natural Sciences of Philadelphia, Philadelphia Pennsylvania (ANSP 421620); Zoological Museum of Moseow State University, Moscow, Russia (Lc-37965) and The Bailey-Matthews Museum, Sanibel, Florida (BMSM 38673) (see Appendix or a complete listing of paratypes).

Type Locality: Aliguay Island, Philippines. Most specimens in the type series were collected by the commercial small-trawl operations off Aliguay Island, at depths of 30–150m.

Geographical Distribution: Presently known from the Central Philippines to Wakayama, Japan (Paratype #23).

Etymology: The specific epithet emphasizes some striking and unexpected similarities to *Conus excelsus* despite the considerable disparity in size.

Remarks: A distingnishing characteristic of this speeies are the spots on the whorls elosest to the suture, which are generally extremely fine in pattern and greater in number than for any other similar species, followed by the thicker, darker brown spiral ribbons at the center of the body whorl. These features are clearly illustrated in the specimens shown in Figure 3. *Conus miniexcelsus* is a distinct species, most easily confused with *Conus praecellens*. However, as disenssed above and shown in Figure 3, the differences in protoconch and early teleoconch morphology between the two speeies are consistent distinguishing characters. This feature puts *Conus miniexcelsus* in the same group as *Conus acutangulus*, *Conus andremenezi,* and *Conus excelsus* (except that the spire of *Conus acutangulus* has strong tubercules at the sutures). *Conus andremenezi* is generally larger, with coarse spots that are purplish brown in color instead of ehestnut. *Conus miniexcelsus* is probably most similar to *Conus excelsus*, although there is a striking difference in size at maturity. The two Japanese specimens examined are more solid and chunky than the Aliguay material. Figure 8 shows the different shape and color of the protoconchs and the eharacteristie switeh in *Conus miniexcelsus* from a conical translueent purplish brown protoconch, to the ivory white first teleoconch whorls, and finally to the normal spotted pattern.

Conus rizali Olivera and Biggs, new species.
(Figures 1, 3, 6)

Description: The speeies is medium-sized; specimens examined are 26–39 mm in length. The shell is biconic, with an unusually tall, straight, and sharply pointed spire and a straight-sided body whorl, sharply angled at the shoulder. Outline narrow (D/L = 0.397 ± 0.011); The larval shell has two whorls, and is *praecellens*-like but somewhat proportionally broader than for most speeimens of *Conus praecellens*; this is followed by two teleoeonch whorls that have a characteristic white-matte surface, somewhat crinkly; starting with the fourth teleoconch whorl, there are 8–9 spotted spire whorls.

The body whorl is characterized by shallow spiral ribbons with only a narrow interstitial space between them; these are broadly spotted in light yellow-brown. Characteristieally, immediately below the periphery, the first spiral ribbon lacks spots, leaving a white zone. Although there is some variation, the spots are much lighter in color than in related forms (Paratype 2 almost completely lacks spots in the body whorl).

Type Material: The Holotype is deposited at the Marine Seience Institute at the University of the Philippines; Paratypes are deposited at the Academy of Natural Sciences of Philadelphia, Philadelphia, Pennsylvania (ANSP 421621); the Harvard Museum of Comparative Zoology, Cambridge, Massachusetts (MCZ 361610) and in the Museum National d'Histoire Naturelle, Paris France (MNHN 21133) (see Appendix for a complete listing of paratypes).

Type Locality: All type specimens were obtained from commercial dealers in the Philippines, and the exact collection locality of the types could not be verified. Springsteen and Leobrara show a figure of *Conus rizali* (labeled *Conus subaequalis*) indicating Punta Engaño, Cebu, suggesting that these were probably collected by fishermen nsing tangle nets at depths of 100–200m.

Geographical Distribution: Philippines.

Figure 3. Three distinctive forms with "*praecellens*-like" protoconchs. Top row is a series of *Conus praecellens*, "sowerbii form". Bottom row is *Conus praecellens*, "Aliguay form". In the middle row are two specimens of *Conus rizali* new species, the Holotype (left) and Paratype 2 (right), both MSI. Measurements provided in Appendix 1.

Etymology: This species is named in honor of Jose Rizal, the National Hero of the Philippines. Dr. Rizal, who was executed by the Spanish Colonial Administration in 1898, collected shells as a hobby.

Discussion: Of all of the similar forms, *Conus rizali* has the most narrow outline (D/L = 0.397 ± 0.011); specimens of *Conus praecellens* from Aliguay, which are generally narrower than the "Sowerbii form" have a D/L = 0.44, and for *Conus miniexcelsus*; (D/L = 0.416) these are both narrower than *Conus andremenezi*.

Although Röckel et al., put this species in synonymy with *Conus praecellens*, we believe that it is a distinctive form that can readily be separated from specimens assigned to *Conus praecellens*. The narrower outline, the shallow ribbons on the body whorl, and differences in protoconch/early teleoconch morphology separate *Conus rizali* from other related forms. *Conus rizali* was previously figured as *Conus subaequalis* Sowerby III, 1870, by authors. This name was used by Springsteen and Leobrera, and by Lim and Wee (1992); however, the specimen recently figured by Robin (2008) as *Conus subaequalis* is not *Conus rizali* but *Conus minexcelsus*. A specimen was also figured by Röckel et al. (Plate 54, Figure 6) but they refer this to *Conus praecellens*. *Conus rizali* is sufficiently distinct so that it can immediately be picked out from other related forms discussed elsewhere in this article: the narrow outline of the shell sets it

immediately apart, and in fact the form that is most similar in outline is *Conus gratacapi* from Japan, which is an unrelated species. This species has only been intermittently collected over the last four decades, and never in large numbers. As has been discussed in detail by Röckel et al., and is shown in the original figure of Sowerby (which Röckel et al., reproduced), the specimens that we assign to *Conus rizali* are clearly not conspecific with the figure of *Conus subaequalis*, which likely refers to a different form in the *Conus praecellens* complex.

Morphological Definition of Species in the *Conus praecellens* Complex: Two "*miniexcelsus*-like" Forms

In this section, we describe and define two distinctive forms in the *Conus praecellens* complex from the Philippines. As will be defined in the Discussion, the "*Conus praecellens* complex" can be divided into two broad groups on the basis of protoconch morphology, the "*praecellens*-like" forms and the "*miniexcelsus*-like" forms.

The two *miniexcelsus*-like forms from Aliguay Island (i.e., those with non-*praecellens*-like protoconchs), which we proposed to designate as new species, are discussed first. The Aliguay specimens of these two forms are easily distinguishable from each other (see Figure 4). Since both of these *miniexcelsus*-like forms were apparently unnamed, these are formally described in the section above. The appendix summarizes the individual type specimens on which the new taxa are based.

Conus andremenezi Olivera and Biggs, new species (Figure 2)

This form may be similar or identical to *Conus bicolor* Sowerby I, 1833, which is a preoccupied name. Sowerby then provided a new name in 1841, *Conus sinensis*. Röckel et al., (1995) stated that "taxonomic status of *Conus bicolor/ Conus sinensis* (Sowerby II, 1841) remains disputable because the type specimen is lost and the type figure (Plate 54, fig. 3) does not match *C. praecellens* in a satisfying way: the pictured shell has a comparatively low spire. . .is somewhat bulbous below the shoulder and its color pattern consists of brown axial flames. . .we favor synonomy with *Conus praecellens*." The figure shown by Röckel et al. (originally drawn from "*Conus bicolor*") is similar to the species we describe above as *C. andremenezi*; we have not adopted the name *Conus sowerbii* for this species because the syntype in the British Museum does not appear to be conspecific with *C. andremenezi*.

We believe that *Conus andremenezi* is clearly distinguishable from typical Philippine specimens of *C. praecellens*; first, the protoconch is not "*praecellens*-like"; second, this form is generally broader and has a characteristic purplish-brown coloration. Furthermore, on the body whorl, there are raised but not flattened spiral ridges that undulate, with a wide space between ribbons with axial scales between the spiral ridges. More consistently, the sculpture on the spiral whorls has narrow, raised ridges, widely spaced from each other. This suite of characteristics consistently distinguishes this species from *C. praecellens* of similar size (see Figure 1) and from *Conus miniexcelsus* (see next species); *Conus rizali* is even more distinctive from *C. andremenezi*. There are a group of small *Conus praecellens* that are most easily confused with *Conus andremenezi*; these are discussed under *Conus praecellens* below.

Conus miniexcelsus Olivera and Biggs, new species (Figure 2)

This very distinctive species is characterized by its relatively narrow shell outline (D/L ≈ 0.42 vs. 0.47 for *C. andremenezi*), the multispiral protoconch of 2.5–3.0 whorls, which is translucent and distinctly brownish or purplish and contrasts in its color with the first 2.0–2.5 teleoconch whorls that are ivory white. In most specimens, these white whorls are smooth or have, at most, nearly obsolete tubercles. This is followed by 6–10 spotted teleoconch whorls that are grooved and have strong axial structure so that the upper part of each spire whorl has a distinctly tiled appearance. The body whorl has shallow spiral ribbons with regular, brown spots that have a characteristic pattern described in the Appendix in detail. The colored, translucent protoconch contrasting in color with the first two shiny-white teleoconch whorls, combined with the slender shape and the very fine spotted pattern are diagnostic of this distinctive species. There is considerable variation in how dark the spots are; a range of variations is shown in Figure 4. A full description of this new species was provided in the previous section; detailed measurements of all the types are provided in the appendix. Almost all specimens have been collected by small trawls in Aliguay from 60–130 m, but occasional specimens have also been collected using gill nets off Balicasag Island. One specimen assigned to this species from southern Japan is included in the type series (Figure 4). Figure 2 makes evident the generally finer pattern and narrower shell shape of *Conus miniexcelsus* compared to *Conus andremenezi*. In addition the spiral ribbons of the body whorl of *Conus miniexcelsus* are smooth, but are distinctly crenulated in *Conus andremenezi*.

Overview and Description of the "*praecellens*-like forms"

Conus praecellens remains a confusing taxon, and the scheme proposed below is not entirely satisfactory; multiple forms have been assigned to this species by various workers. Even after the two "*miniexcelsus*-like forms" are separated as new species, what remains still comprises a confusing set of specimens, most of which we are provisionally retaining in *C. praecellens*. We believe that the retention of diverse forms within *C. praecellens*

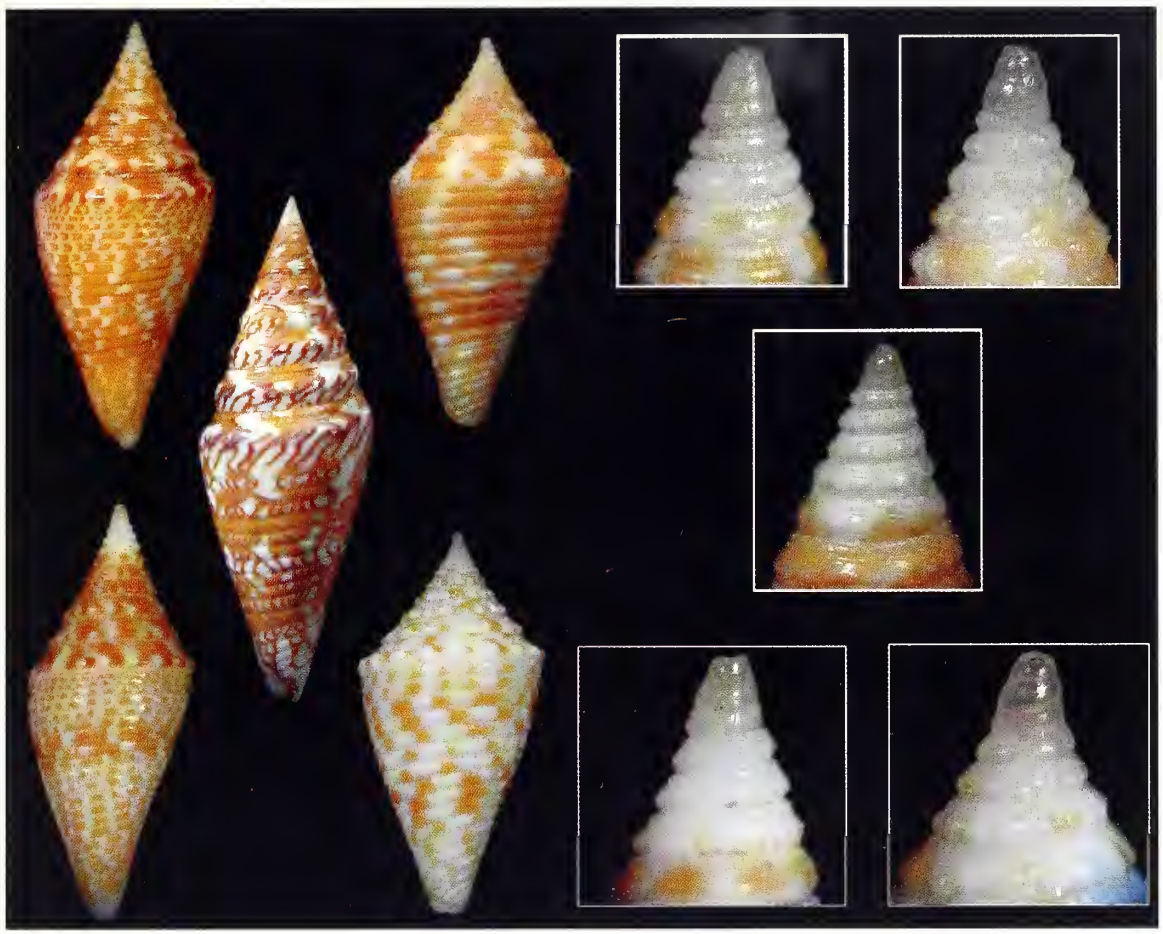

Figure 4. An illustration of the "*miniexcelsus*-like complex". Shown are five specimens (left five) and close-ups of their respective protoconchs (right five). Left, top and bottom: Conus *miniexcelsus* (Paratypes 2 and 18, respectively), middle: Conus *excelsus*, and right top and bottom: Conus *acutangulus*. Measurements provided in Appendix 1.

will prove to be only an interim solution, and new morphologically similar species will be identified once a more extensive molecular and morphological analysis has been carried out over a wider suite of specimens from a greater geographic range.

There is a widely illustrated specimen designated as "a possible syntype" of *Conus praecellens* from the British Museum. This is atypical of specimens assigned to *C. praecellens* from the Philippines. This possible syntype from the China Sea is lighter in color and finer in sculpture on the body whorl than either of the two major Philippine varieties that we include in *C. praecellens*. The first group, "the Aliguay form," which is small and light colored, has been extensively collected both by the small dredge operations in Aliguay Island, and is the form illustrated in Figure 3. A second more variable group that we refer to as the "sowerbii forms," include larger specimens that vary considerably in shell pattern, shape, and size. These comprise most specimens collected by fish trawlers in the period from 1955–1965, particularly from two localities, Tayabas Bay and Maqueda Bay. A third group is that referred to by previous authors as *Conus subaequalis* and is described above as *Conus subaequalis*. The three forms are shown in Figure 5.

Conus praecellens "Aliguay form"
(Figure 3)

The series of specimens that we assign to *C. praecellens*, "Aliguay form", appears to be the closest to the type in the BMNH in shell pattern; these have mostly been collected in 30–80 fathoms off Aliguay Island, between Mindanao and Bohol in the Philippines. The Philippine specimens are smaller than the BMNH "syntype" (average size ≈ 24mm); key features that distinguish this form are a blunt, paucispiral protoconch of two whorls, the relatively smaller size, and the chestnut color of the spots. Details of the spire sculpture and body whorl that are also diagnostic are delineated below.

The shells of this form (see Figure 5) typically have 2.0–2.5 protoconch whorls, the first being quite spherical and inflated, and the second narrower and more elongate. The first two teleoconch whorls are typically white and flattened compared to the protoconch whorls, and they are knobbed on the periphery, while the two

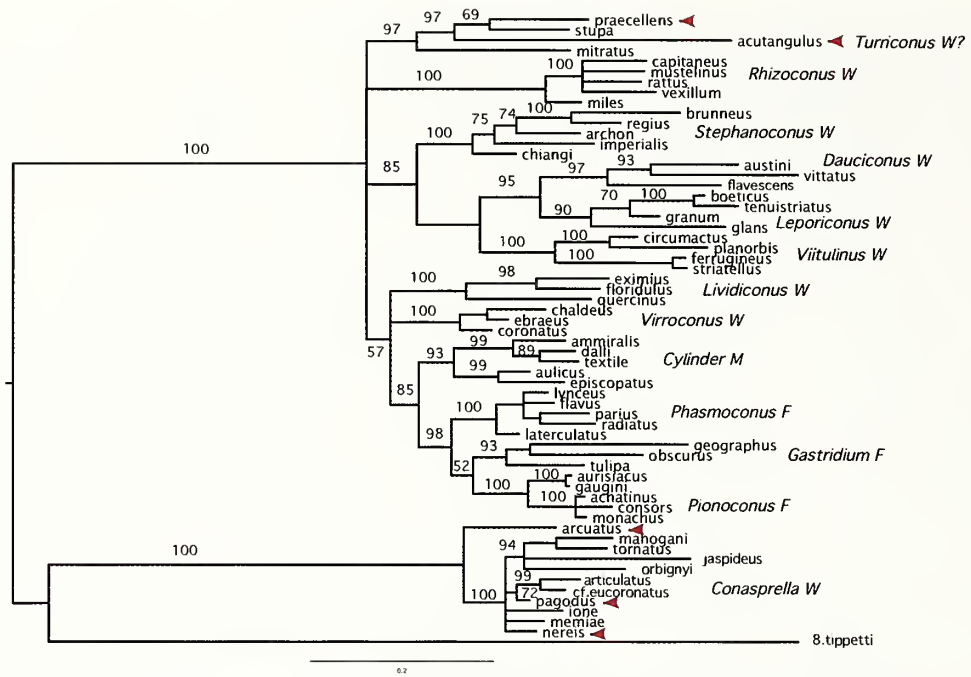

Figure 5. Phylogenetic tree of some *Conus* species based on 12SrRNA sequences. Species shown in Figure 1 are indicated with arrows. Branches are labeled with Bayesian confidence values (posterior probabilities expressed as percentages). These data clearly separate *Conus acutangulus* and *Conus praecellens* from the *Conasprella* species with 100% confidence and join them with *C. stupa* and *C. mitratus* with 97% confidence.

protoeoneh whorls are smooth. There are 8 to 9 whorls spotted with a chestnut brown eolor, with the first one or two spotted whorl(s) also knobbed. The early teleoeonch whorls are eharaeterized by a deep spiral groove on the upper seetion of the whorl; these spiral grooves gradually inerease in number as the whorls get larger; these are narrow furrows that ean be bisected by axial sculpture that varies considerably in strength; in speeimens where the axial sculpture is strong, the area immediately adjacent to the suture looks as if it were tiled, since the eombination of the spiral grooves and the axial seulpture divide the area between grooves into square sections. The broader part of the spiral whorl is smooth to the periphery; the lower suture is below the sharply angled periphery.

Conus praecellens "sowerbii forms"
(Figure 3)

There are forms in the *C. praecellens* complex most commonly found in collections; most specimens were eollected by trawlers aromnd 1960 in great numbers in the Maqueda and Carigara bays of Samar Island, and in Tayabas Bay of Southwestern Luzon, from Jolo Island in the Sulu Sea. The "sowerbii forms" are larger and more densely spotted than the specimens of the "Aliguay form" described above. There is considerable variation in shell morphology: some specimens are slender and narrow with fine sculpture; others appear to be much broader at the shoulders with an overall coarser sculpture. However, when preserved, the protoconchs of all of these have the typical highly inflated first whorl, with only two, pearly white protoconeh whorls. A range of speeimens eolleeted from various Philippine loealities, all with typieal "*praecellens*-like" protoconehs that are well preserved are shown in Figure 5 (the contrast between these and the "Aliguay form" is also illustrated in that figure).

Given the distinctive (and mutually similar) protoeonehs of both the Aliguay and the "sowerbii forms," we have provisionally assigned these in *C. praecellens*. However, further characterization of both the radular and gut morphology, as well as a molecular eharaeterization, may prove that these are distinet from each other, and that there are additional separable species embedded in the "sowerbii forms", a possibility that elearly needs to be further evaluated.

Conus praecellens, other distinetive varieties.

A smaller form of *Conus praecellens* was reeently collected by MNHN, off Aurora, Eastern Luzon, Philippines. These specimens were notable beeause they were very similar to *Conus andremenezi*, but much smaller. They are easily separable from *Conus andremenezi* beeause they have the typieal "*praecellens*-type" protoeonch. These look very different from the two *Conus praecellens* "forms" described above. We note that in general, *Conus andremenezi* is a larger species; however, there have been juvenile *Conus andremenezi* speeimens collected using *lumum-lumum* nets in the Camotes Sea, along with specimens of the *Conus praecellens*, "Aliguay form," described above. It seems likely that only juvenile speeimens of *Conus andremenezi* are collected at this

locality because *lumun-lumun* nets were used, and it presumably takes longer than the three months *lumun-lumun* nets are laid out for *Conus andremenezi* to reach full maturity. These small specimens of *Conus andremenezi* do have the characteristic protoconchs of that species, though they are somewhat lighter in color than the Aliguay series. In contrast, the variety of *Conus praecellens* collected off Aurora (trawled at 83 m depth) have the *praecellens*-type protoconch. At the same site, the MNHN expedition collected two dead, somewhat eroded specimens, that were larger in size, in a trawl 189–307 meters in depth that are likely to be true *Conus andremenezi*.

In addition, a species was recently described as *Conus beatrix*, Poppe and Tagaro, 2006. We have not had an opportunity to examine the Holotype of this species; it may be that these represent a series of unusually pale specimens, possibly continuous with the *Conus praecellens* "Aliguay form", described above. If this were the case, and further molecular evidence shows that these are separable from *Conus praecellens*, then these authors would have provided a potentially valid species name for *Conus praecellens* "Aliguay form."

Conus rizali Olivera and Biggs, new species
(Figure 3)

This distinctive species was previously recognized by Springsteen and Leobrera (1986) and by Lim and Wee (1992) as morphologically separable from any of the other forms assigned to *C. praecellens* or *C. acutangulus*. In their treatment of this complex, Springsteen and Leobrera (1986) provided a figure of this form, to which the name *Conus subaequalis* Sowerby III, 1870, was assigned, with the locality Punta Engaño, Cebu, Philippines. This locality suggests that the specimens they examined were collected by gill nets in deep water. A similar specimen was illustrated by Röckel et al. (plate 54, figure 6) and labeled "*Conus praecellens*" from Davao, Philippines (likely collected by tangle nets off Balut Island, Davao). In our description of *Conus rizali* (see above), the name we propose for this form, we discuss a number of distinguishing morphological characteristics. The name assigned by both Springsteen and Leobrera and Lim and Wee, *Conus subaequalis* does not appear to refer to this form (Röckel et al. reproduce the original figure of Sowerby which refers to a smaller shell, broader in outline with seemingly more deeply colored spots than *Conus rizali*.)

The slender, high-spired, and biconical shape of *C. rizali* is similar to the Japanese *Conus gratacapai*, a poorly understood, rare, deep-water species. Several museum specimens of *C. gratacapai* were examined, including some Paratypes of the latter. Several striking morphological differences indicate that the two forms are not conspecific. Most notably, *C. gratacapai* does not have the sutural structure of *C. rizali*; there is a smooth transition between whorls in the former, but a peripheral overhang between spire whorls in the latter. Another obvious difference are the light brown spots of *C. rizali*, which are absent in *C. gratacapai* Pilsbry, 1904. The spire sculpture of the two forms differs significantly as well.

Other "*miniexcelsus*-like" forms: *Conus excelsus* and *C. actangulus*.

The presence of a translucent multispiral brownish or purplish protoconch, followed by several ivory white teleconch whorls is a striking morphological feature of *Conus minexcelsus*. In this respect, two well-known species are "*miniexcelsus*-like": *C. excelsus* and *C. acutangulus*. Both have the same characteristic translucent protoconch and ivory white early teleconch whorls (see Figure 6). All of these forms have the body whorl covered by spiral ribbons. The major difference is in the highly nodulose whorls of *C. acutangulus*, versus the smoother whorl of *C. minexcelsus*. *Conus excelsus* is somewhat intermediate in this respect. There are also the striking and obvious differences in size, *C. excelsus* being by far the largest. Although the shells are different in pattern and size at maturity in these three species (Figure 4), note the similar purplish brown translucent protoconchs, followed by the ivory white early teleoconch whorls before the regular shell pattern is initiated. Typical *Conus acutangulus* (Figure 4, top right) and the "deep-water form" (Figure 4, bottom right) are both distinctly more nodulose while there is a striking similarity between *Conus excelsus* and *Conus miniexcelsus* in their protoconchs and early teleoconch whorls.

Conus excelsus Sowerby III, 1908
(Figure 4)

This is one of the largest species in the group (to over 100 mm). The protoconch consists of about 3.25 whorls, with a maximum diameter of about 1 mm. The protoconch whorls are grayish, and early teleoconch whorls are bright white that then begin to have brown radial blotches of varying size in the later whorls. Early teleoconch whorls have one deep spiral groove, increasing to up to 4 spiral grooves in the later whorls. Although body whorl can be almost smooth, some specimens have variably spaced, axially striate spiral groups separated by granulose ribbons. Most specimens in the Philippines are from Balut Island, Davao, collected by gill nets at depths of approximately 100–150 fathoms. Although *C. excelsus* is strikingly different in size, the body whorl sculpture, the protoconch and early teleoconch whorls show such strong similarities to *C. miniexcelsus* that a close genetic relationship between the two species seems highly likely.

Conus acutangulus Lamarck, 1810
(Figure 4, 6)

Among Philippine specimens, there appear to be two varieties of *Conus acutangulus*, the "typical form" (Figure 4, top row, right), which conforms to the neotype designated by Kohn (Kohn, 1981) and a variety that we will refer to as the "deep-water form" (Figure 4, bottom row, right). This is a well-known species, and the only

Figure 6. Distinctive forms proposed to belong to the *Turriconus* clade. Top row (showing the shell and, in the inset above it, a close-up of the corresponding protoconch), from left to right: *Conus excelsus*; *miniexcelsus* (Holotype); *acutangulus*, "typical form"; *acutangulus*, "deep-water form"; *andremenczi* (Holotype); *praecellens*, "sowerbii form"; *rizali* (Holotype); *praecellens*, "Aliguay form". Lower row, from left to right: *Conus stupa*; *stupella*; *mitratus*; *cylindraceus*. The protoconch of *Conus stupa* is not shown; it is extremely eroded in the figured specimen. Measurements provided in Appendix 1.

issue is whether the two distinct forms described below are conspecific or not

"Typical form" (description after Röekel et al., 1995): This is a small to medium sized shell; the larval shell is multispiral with 3 to 4 whorls. The teleoconch whorls are strongly tuberculate for at least the first eight post-nuclear whorls, a distinctive characteristic. The body whorl has strong spiral ribbons or ribs that are separated by grooves with strong axial threads. The shell is largely brown, except for small, scattered white blotches at the shoulder and center. The aperture is white. This form is collected in relatively shallow water, typically between 3–20 m. Divers in Batangas Bay, Luzon, collected most Philippine specimens; more recently divers in Nucnuean, Bohol, have collected the typical form. Fully mature specimens are 25–38 mm in length, D/L ≈ 0.50–0.53. Typical fully mature non-Philippine specimens are also illustrated by Röckel et al. 1995 (plate 54, figs. 19 and 21).

"Deep-water forms:" The deep-water varieties typically occur between 30 to 150 meters, and are collected either by dredging or gill nets. These forms do not have the brown to dark brown color of the typical variety, but are mostly white with sparse light orange-brown or grayish flecks. Generally smaller than the typical form, most specimens are 16–22 mm in length. This form has been collected in Aliguay and Pamilacan Islands. A comparison of available deeper-water specimens assigned to *C. acutangulus* reveals considerable variation that needs to be more carefully investigated and defined. These forms clearly occur outside the Philippines; Röekel et al., illustrate a specimen from the Solomon Islands (plate 54, fig. 17).

Molecular Phylogeny: Relationship of *Conus praecellens* to Other High-spired *Conus* Species

Most of the forms investigated in this article were collected in the Central Philippines, primarily by gill nets or trawlers offshore. A number of smaller *Conus* species of similar shape, including several diverse forms assigned to *Conus praecellens*, are collected in this way (Figure 1). As described above, in most taxonomic work, *Conus praecellens* is either explicitly discussed or implicitly grouped with similarly shaped, high-spired, small,

deep-water *Conus* species even when authors do not endorse a specific phylogenetic scheme (for example see Robin, 2008; Röckel et al., 1995; Walls, 1979).

Table 1 summarizes previously proposed taxonomy based on shell morphology, which can be assessed using molecular data. For comparison, a phylogenetic tree based on 12S mitochondrial DNA includes *Conus praecellens* and *C. acutangulus*, along other vermivorous, molluscivorous, and piscivorous *Conus* species (see Figure 5).

This molecular phylogeny assigns *C. praecellens* and *C. acutangulus* to the same clade. The surprising, yet clear-cut, result is that most other species proposed to be included in *Conasprella* with *C. praecellens* by previous workers based on shell morphology actually cluster in a branch extremely divergent from most *Conus*. The type species of *Conasprella*, *C. pagodus*, is on this very distant branch, which we refer to as the "*Conasprella* clade". Additional molecular data support these findings (Bandyopadhyay et al., 2008). These data, discussed below suggest that the degree of divergence makes it untenable to keep these species (*C. pagodus*, etc.) within the same genus as other *Conus* species.

Definition of a Clade Based on Morphological and Molecular Data: The combination of the morphological analysis of the various species and distinctive forms above combined with the available molecular data (Figure 5) provides a framework for defining the group of *Conus* spp. most related to *C. praecellens* and *C. acutangulus*. As discussed above, some of the superficially similar high spired *Conus* species are not at all closely related based on the molecular data. In the Philippines, there are ten species and 12 distinctive forms which we assign to this group that we designate the *Turriconus* clade (*Conus excelsus* = *Conus nakayasui*, type species). A comprehensive taxonomic revision of the genus *Conus* is currently being carried out by A. Kohn; we suggest that *Turriconus* is a distinct branch within the major group of species that together, comprise the genus *Conus*.

The molecular work definitively excludes a number of *Conus* spp. from *Turriconus*; clearly, species such as *Conus pagodus*, *Conus memiae*, *Conus nereis*, and other deep-water species with high spires such as *Conus boholensis* (Petuch, 1979), *Conus cugrammatus* (Bartsch and Rheder, 1943), as well as non-Philippine species such as *Conus jaspideus* (Gmelin, 1791) and *Conus arcuatus*, though morphologically similar to *C. praecellens*, do not belong in the *Turriconus* clade. The 10 species and 12 distinctive forms that comprise the *Turriconus* clade in the Philippines are shown in Figure 6, and summarized in Table 2; as outlined in the table, these fall into four groups that will be discussed in turn.

The first group is the *excelsus/acutangulus* group (Group I), with four species and five distinctive forms. This group includes the type of *Turriconus*, *Conus excelsus*. The second is the *praecellens* group with two species and three distinctive forms. The third is the *mitratus* group of at least two species and fourth, the *stupa* group.

Table 2. Morphologically distinctive "forms" in the *Turriconus* clade (*Conus excelsus*, type species).

Group I	*Conus excelsus*
	C. miniexcelsus
	C. andremenezi
	C. acutangulus "typical form*"
	C. acutangulus "deep water form"
Group II	*C. praecellens* "sowerbii forms"*
	C. praecellens "Aliguay form"
	C. rizali
Group III	*C. mitratus**
	C. cylindraceus
Group IV	*C. stupa*
	C. stupella *

*Peptide toxins belonging to the O-superfamily have been determined for these "forms."

The first group of species, the *excelsus/acutangulus* group, is characterized by a generally conical protoconch, without the spherical, inflated first protoconch whorl. The protoconch is translucent, brownish purplish or light yellowish in color; and followed by two or more, much whiter, teleoconch whorls. The four species in this group are *Conus excelsus*, *Conus miniexcelsus*, *Conus andremenezi*, and the two forms of *Conus acutangulus* described above.

In the second group, the *praecellens* group (Group II), the characteristic feature is a white protoconch of two whorls, with the first protoconch whorl being inflated and spherical (i.e., "*praecellens*-like"). The characteristic shape of this protoconch is diagnostic of this group (as shown in Figure 6); there may be more species than are recognized here, since this is a rather variable assemblage of forms as is discussed above. *C. praecellens* and *C. rizali* are the two species in this group, with at least two distinctive forms assigned to *C. praecellens*.

The third group in *Turriconus*, based on molecular data and expanded using morphological similarities, is the *Conus mitratus* group (Group III). These species have much more elongated body whorls than are found in the two groups above. They seem to share the characteristic white early teleoconch whorls before the mature coloration is expressed with the first group. On morphological grounds alone, we assign two species to this group: *Conus mitratus* and *Conus cylindraceus* (Broderip and Sowerby, 1830). The molecular evidence in this paper is only provided for *Conus mitratus*; however, corroborative molecular evidence for *Conus cylindraceus* has been obtained by others (C. Meyers, personal communication).

The fourth group in the *Turriconus* clade is a subgenus (*Kurodaconus*) (Group IV) recognized as distinctive by some workers; the molecular evidence suggests these species should be included in *Turriconus*. There are two species in this group, *Conus stupa* and *Conus stupella*; it is the opinion of several workers on *Conus* that these may not be separable species, since they always appear to occur together. This suggestion needs to be further evaluated. These forms differ from Groups I and II by the smooth body whorl, while the species in these groups have the spiral ribbons or ribs.

The overall hypothesis, based on the combined molecular and morphological data, is presented in Table 2. We used this working hypothesis as a guide to analyze toxins in the putative species of the *Turriconus* clade, from which DNA samples were available (marked by asterisks in Table 2).

Using Toxinological Markers to Evaluate the *Turriconus* Clade: The hypothesis presented in Table 2 was experimentally tested using a toxinological analysis. Since cone snails are venomous animals, they use toxins in their venom to capture prey, defend against predators and for competitive interactions. Since each species presumably has a different spectrum of prey, predators and competitors, the genes encoding venom components are "exogenes," which diverge very rapidly as new species evolve. The peptide toxins that are present in *Conus* venoms are encoded by only a few gene superfamilies; these are predicted to undergo accelerated evolution.

Conus peptide genes are examples of exogenes (Olivera, 2006); their gene products act exogenously, targeting other animals (instead of acting endogenously within the cone snail itself). A considerable amount of prior work has demonstrated that each *Conus* species has its own distinct complement of venom peptides, with the same peptides not found in venoms of even closely related species. What would be predicted when a group of closely related species is analyzed is that the gene products encoded by a particular conopeptide superfamily will be highly related to each other, but not identical in sequence. This toxinological prediction was used to test if the species proposed to be in the *Turriconus* clade do indeed have closely related (but not identical) toxins, as would be expected for exogene products.

All species for which DNA was available were analyzed; since no complementary DNA (cDNA) samples were available, the analysis had to be carried out on genomic DNA. The gene superfamily used for the analysis was the O-superfamily; it is possible to determine the sequence of the mature toxins because there is a conserved intronic sequence that borders the mature toxin region (see Materials and Methods) thus, PCR primers can be used to determine peptide toxin sequences from each species. The O-superfamily has diverged into two branches (Olivera et al., 1999; Terlau and Olivera, 2004) one hydrophilic, which includes the ω- and κ-conotoxins from fish hunting cone snail venoms (the "ω-branch") and the second highly hydrophobic; in fish hunting cone snails this includes the δ and μO-conotoxins (the "δ-branch"). PCR primers used to amplify genes in each branch are different and therefore toxin sequences can be separately obtained. This analysis was carried out and the results are shown in Figure 7.

It is clear from the figure that representatives of all four species groups, separated using our aforementioned morphological/molecular phylogenetic analyses, yielded homologous O-superfamily peptide sequences that fall into both the ω- and the δ-branches; all of which share a high degree of sequence identity. Moreover, as predicted

Homologous Peptide Toxins from the O-superfamily

ω - screen

C. acutangulus At6.1
CGGRRAPCRQYIQCCSHSCNTFLGTCV*
C. praecellens Pr6.1
CGSPRARCRQYLQCCSRHCNKFLGMCV*
C. mitratus Mp6.1
CGGPQAPCRQYSQCCSRVCNKFFNKCR*
C. stupa Sa6.1
CGPPRARCRQYLQCCSRRCIKFLNMCM*

δ - screen

C. acutangulus At6.7
DECLAGSEFCGFLKIGPPCCSGYCLFVCL*
C. mitratus Mp6.7
ECRANGATCGILKPGAKCCDGWCFFVCIG*
C. praecellens Ps6.7
RDDDCVAGGQGCGFPKIGGPCCSGWCFFVCT*
C. stupa Sa6.7
ECFPKDTFCGFPSSGAPCCSGWCFVVCA*

Figure 7. Toxinological analysis. Predicted mature toxin sequences from two distinct branches of the O-superfamily of conopeptides for four members of *Turriconus*: *Conus acutangulus, Conus mitratus, Conus praecellens,* and *Conus stupa*. An independent comparison of the toxin sequences from the two branches, the hydrophilic ω and the hydrophobic δ, each demonstrate the close relationship between the different species of the *Turriconus* clade analyzed.

by the exogenomic hypothesis (Olivera, 2006), these peptide sequences have diverged from each other. Therefore, the postulated accelerated evolution of these exogenes, which, in turn, is an indicator of species divergence, is indeed observed.

DISCUSSION

This study has used three types of data: comparative morphology, molecular phylogeny based on standard gene markers, and toxinological markers (i.e., peptide toxin sequences). This three-pronged effort was aimed at branch definition leading to a specific phylogenetic hypothesis. As is typical, none of the individual data sets were as comprehensive or complete as might be desired; nevertheless, the combination made the phylogenetic framework proposed a compelling one.

Morphological Evidence: Importance of the Protoconch/Early Teleoconch. Springsteen and Leobrera (1986), separated two forms in the *C. praecellens* complex from the Philippines, the commonly trawled form (designated *Conus sowerbii*), and a second, much more slender form, with lighter yellowish brown spots, assigned to *Conus subaequalis* (*op. cit,* pl. 71, figs. 1, 2). This treatment was subsequently adopted by Lim and Wee (1992). Thus, while Walls (1979) and Röckel et al., only recognized *C. praecellens* and *C. acutangulus*, these workers recognized three distinctive forms from the Philippines/Southeast Asia

("*C. sowerbii*" (= *C. praeecllens*), "*C.subaequalis*," and *C. aeutangulus*).

One reason why the definition of forms has been challenging is because most available specimens did not have good protoconch (or early teleoconch) whorl preservation. Philippine specimens in this group from many localities have a dark periostracum layer covering the spire of the shell, which is routinely removed by commercial shell dealers using acid, a treatment that destroys key features critical for morphological differentiation. In the analysis below, we used these "compromised" specimens in our morphometric analyses but focused primarily on the few specimens with well-preserved protoconch and early teleoconch whorls for discriminating between forms. Once consistent differences in protoconch and early teleoconch morphologies were established, additional morphological characters were used to help separate distinctive forms. This general approach was used for the morphological definition of forms described above.

The basic approach is illustrated in Figure 8, which show two forms collected off Aliguay Island; these have proven to be particularly illuminating. Both would have been assigned by Röckel et al. (1995) to *Conus praeecllens*. In Figure 8, the specimen on the right is a specimen of what we refer to as the "Aliguay form" of *C. praeecllens*; the other specimen (on the left) is *Conus miniexeelsus* new species. The top section of Figure 8 shows the shells of the two specimens of approximately same size. Although their shell patterns differ, the considerable variation observed in this complex led to a rather confused situation in the past. The major morphological observation that changed this situation is illustrated in the lower section of Figure 8, which shows a magnified view of the well-preserved protoconch and early teleoconch whorls of the two specimens; we believe that the differences depicted are sufficiently diagnostic to definitively assign the specimens illustrated into two distinct groups (i.e., *Conus praeecllens* and *Conus miniexeelsus*). The multispiral brownish protoconch of *C. miniexeelsus* contrasts with the protoconch of the specimen assigned to *C. praeecllens*; the early teleoconch whorls are also distinctively different. Using these as the major criteria for separating forms makes it simpler to identify other shell morphological characteristics that consistently differ, even though each individual character might have a considerable range of variation. This approach has provided a much more consistent suite of characters to allow a definition of different morphospecies.

Using these criteria, the Philippine forms previously assigned to *C. praeecllens* fall into two separable groups: a group that has a characteristic protoconch of 2.0–2.5 whorls, with a rounded and somewhat inflated first whorl; the protoconchs of these forms are pearly-white; we have referred to these as the "*praeecllens*-like forms." The specimens that do not have this very characteristic type of protoconch, herein collectively referred to as the "*miniexeelsus*-like forms", have the first protoconch whorl not rounded, nor inflated. The entire protoconch of the latter generally has a more triangular (conical) outline when compared to the "*praeecllens*-like forms;" these protoconchs are typically translucent-brown, translucent-yellowish or off-white. Although this color can be subtle, the contrast to the pure-white early teleoconch whorls is usually diagnostic.

Figure 8. Comparison of two morphospecies collected in Aliguay Island, Philippines. The specimen at the left is *Conus miniexcelsus* (Holotype), and on the right is *Conus praeecllens*, "Aliguay form". Top: The whole shell. Bottom: Close-up of the protoconch and first few teleoconch whorls.

THE MOLECULAR EVIDENCE

A major conclusion from the molecular analysis is that *C. praeecllens* and *C. aeutangulus* do not belong in the *Conasprella* clade. Instead, they form a distinct branch among the major group of species in *Conus*. Another unexpected result from the molecular phylogenetic analysis is the other species, *Conus stupa* and *Conus mitratus*, branch within the same well-supported clade as *C. aeutangulus* and *C. praeecllens*. In particular, *Conus mitratus* has strikingly different shell morphology from *C. praeecllens* and *C. acutangulus*. In all previous taxonomic work, *Conus mitratus* and *Conus stupa* have

been assigned to different subgenera from *Conus praecellens* and *Conus acutangulus*.

The Contribution of Toxinological Markers. Our starting point for defining the clade of cone snails that includes *Conus praecellens* were the previous proposals in the literature for subgenera (or genera, when *Conus* was split into multiple genera) that included *Conus praecellens*. In most proposals, *Conus praecellens* was, in effect, proposed to be related to other high-spired, deep-water species such as *Conus pagodus*, *Conus memiae*, and *Conus arcuatus*, which are usually assigned to *Conasprella*. In some of the prior hypotheses, this group of species was split in two; e.g., *Conasprella* and *Kermasprella* (da Motta, 1991), or *Conasprella* and *Endemnoconus* (Okutani, 2000). Although these various proposals differ in detail, they all group *C. paraecellens* and *C. acutangulus* with species such *C. pagodus*, *C. memiae* and *C. arcuatus*. However, both the molecular phylogenetic results using standard molecular markers and the exogenomic data using toxinological markers are inconsistent with all of these hypotheses; only *Conus praecellens* and *Conus acutangulus* appear to be closely related to each other by the latter two criteria. All of the other species previously grouped with *Conus praecellens* in prior phylogenetic proposals based on shell morphology are now assigned to a distant and different branch of cone snails from *Conus praecellens/Conus acutangulus* (see phylogenetic tree in Figure 2).

Instead, the combined data led to a new and strikingly different phylogenetic framework for the *Conus* species comprising the branch that includes *Conus praecellens*; this proposal is summarized in Figure 7 and Table 2. An entirely unexpected set of species appears to be more closely related to *Conus praecellens* (in Groups 3 and 4 in Table 2). These *Conus* species (*C. stupa*, *C. stupella*, *C. mitratus*, and *C. cylindraceus*) were never previously proposed to be in the same clade/subgenus as *C. praecellens* and *C. acutangulus*.

The use of toxinological markers has buttressed the molecular phylogenetic analysis. The presence of highly similar peptide toxins that belong to the O-superfamily of conopeptides indicates that the various groups that branch together with *Conus praecellens* are indeed related, using an independent toxinological data set.

THE *TURRICONUS* CLADE: OVERVIEW

A more comprehensive morphological analysis reveals that various distinctive forms previously assigned to *Conus praecellens* are likely not conspecific; three new species were described and additional distinct forms defined. Thus, *Conus praecellens* and the newly described species, *Conus miniexcelsus*, *Conus rizali*, and *Conus andremenezi* are now proposed to be species in the same clade.

Finally, the morphological analysis focused on the importance of protoconch/early teleoconch whorl morphology. These morphological characters strongly suggest that Group I in Table 2 should include *Conus excelsus* given its strikingly similar protoconch/early teleoconch morphology to *C. acutangulus* and *C. minicxcelsus*. Clearly, there is a difference in size: *Conus excelsus* is much larger at maturity. We would predict that the molecular phylogeny and toxinology of *C. excelsus* will reveal a particularly close affinity to *Conus miniexcelsus* (which is, in part, the basis for the proposed name of the latter). Unfortunately, *Conus excelsus* is rare and we have been unable to obtain a live specimen to date. However, we propose to call the entire group the *Turriconus* clade, with *C. excelsus* as the type species. In terms of species diversity, it would appear that Groups 1 and 2 in Table 2 are the dominant species groups of this clade — except for the differences in protoconch morphology detailed above, they are all high-spired species with the body whorls characterized by spiral ribs or ribbons. *Conus excelsus* is the type species of the subgenus *Turriconus*.

All three types of data used for this investigation need to be expanded. A more extensive molecular phylogeny needs to be carried out on all of the forms indicated in Table 2, including, in particular, the designated "distinctive forms" so that an evaluation of whether these are separable species can be carried out. The new species we have proposed need to be rigorously evaluated both by the standard molecular markers as well as by their toxin genes. More refined molecular phylogeny should also allow a better resolution of how the various forms in the proposed *Turriconus* clade are related to each other and to other species of *Conus*. In addition, the exogenomic analysis, while in agreement with the molecular phylogeny, also needs to be extended to all of the species in the *Turriconus* clade, as well as to other gene superfamilies expressed in venom ducts (in addition to the O-gene superfamily that was shown in Figure 8). The determination of venom peptide sequences by this type of analysis is, in itself, of considerable intrinsic value, since it would allow the predicted gene products from each species to be chemically synthesized and directly tested for functional activity. Finally, the morphological analyses to date are based only on shell morphology. Clearly, other morphological features, particularly the internal anatomy, need to be evaluated; these will serve as an independent test of the phylogenetic hypothesis presented. Potentially, mutually shared and distinctive morphological features of species in this clade of *Conus* may be discovered.

The interaction between the three prongs that are the basis of the approach used in this manuscript has a potential synergy that goes beyond clade definition. The morphological analysis of distinctive forms within the *Conus praecellens* complex identifies candidates that may or may not be different species, separable from the ones already recognized. Using standard molecular phylogeny will help to define this; however, using exogene analysis should be even more definitive: if these were indeed separable species, then none of the toxin gene products should exactly overlap in their sequence,

because of the hypermutation in exogenes that accompanies speciation events.

If a distinctive form was truly a separable species, different toxin sequences would be predicted — if it were merely a variant of the same species, then identity in most venom peptide sequences should be found (except for allelic differences). In some of the well-known species (e.g., *Conus textile*, Linnaeus, 1758, and *Conus striatus* Linnaeus, 1758) that are distributed all over the Indo-Pacific, it has been shown that major venom peptides have the same sequence, even from variants whose shells may be distinguishable from each other because of the long period it may have taken for a species to spread across the entire Indo-Pacific, from the Red Sea to Hawaii.

The inclusion of exogenes in the investigation of biodiversity has a significance that goes beyond differentiating between morphologically closely related species. The divergence of exogenes from one species to the next is indicative of different biology, shaped by different selection pressures. This is essentially a molecular readout of the deeper biological/historical/ecological differences between species that might look morphologically similar. Thus, the characterization of toxin genes in the case of *Conus* not only serves as a tool for branch definition, but is a potentially important entry point toward a more profound understanding of the biological differences between species, a molecular readout that could provide insights into the complex changes that accompany the speciation events that give rise to a biodiverse lineage of animals such as the cone snails.

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APPENDIX

Baldomero M. Olivera and Jason S. Biggs

Conus andremeuezi, summary of type speeimens (Figures of types are eross-referenced)

	Length	Width	Loeality (PI)	Depository (Cat#)
Holotype (Figs 1, 2, 6)	36.7	16.9	Aliguay	MS1
Paratype 1	52.9	21.7	Aliguay	*
Paratype 2	40.1	29.1	Aliguay	*
Paratype 3	40.6	20.1	Aliguay	*
Paratype 4	43.1	22.0	Aliguay	*
Paratype 5	42.7	20.4	Aliguay	MCZ 361611
Paratype 6	26.8	12.4	Aliguay	*
Paratype 7 (Fig 2)	29.4	14.0	Balicasag ls.	Lc-37964
Paratype 8	44.0	20.9	(Philippines)	*
Paratype 9	46.9	20.9	(Philippines)	*
Paratype 10	28.7	13.6	(Philippines)	*
Paratype 11 (Fig 2)	23.0	10.7	(Philippines)	MS1
Paratype 12	29.6	13.0	(Philippines)	FMHN 312461
Paratype 13	33.2	15.4	(Philippines)	BMSM 38672
Paratype 14	26.0	12.6	(Philippines)	*
Paratype 15	43.3	21.4	(Philippines)	*
Paratype 16	26.6	13.1	(Philippines)	*
Paratype 17	31.5	14.6	(Philippines)	*
Paratype 18	39.5	18.5	Aliguay	*
Paratype 19	35.8	17.1	Aliguay	ANSP 421619
Paratype 20	27.7	13.1	Aliguay	*
Paratype 21	30.5	15.4	Aliguay	*
Paratype 22	29.2	13.8	Panglao ls.	MNHN 21131
Paratype 23	46.9	21.8	Olango ls.	*
Paratype 24	37.4	16.7	Aliguay	*
Paratype 25	36.4	17.6	Aliguay	*
Paratype 26	34.6	15.4	Aliguay	*
Paratype 27	44.6	21.9	Aliguay	*
Paratype 28	48.7	22.3	Aliguay	*
Paratype 29	38.6	18.7	Aliguay	*
Paratype 30	33.9	15.3	Aliguay	*
Paratype 31	35.1	15.4	Aliguay	*
Paratype 32	42.5	20.1	Aliguay	*
Paratype 33	35.2	17.0	Aliguay	*
Paratype 34	37.3	17.6	Aliguay	*
Paratype 35	36.8	17.7	Aliguay	*
Paratype 36	21.6	9.3	Camotes Sea	*
Paratype 37	23.8	11.2	Camotes Sea	*

Conus uiniexcelsus, summary of type specimens

	Length	Width	Loeality (PI)	Depository (Cat#)
Holotype (Figs 1, 2, 6, 8)	22.0	19.6	Aliguay	MS1
Paratype 1	27.7	11.8	Aliguay	*
Paratype 2 (Fig 2)	27.3	11.6	Aliguay	MS1
Paratype 3	29.0	12.5	Aliguay	*
Paratype 4	27.4	10.8	Aliguay	*
Paratype 5	28.3	11.4	Aliguay	*
Paratype 6	25.5	10.5	(Philippines)	*
Paratype 7	31.1	11.6	(Philippines)	Le-37965
Paratype 8	31.5	13.1	(Philippines)	FMNH 312462
Paratype 9	28.9	12.3	(Philippines)	*
Paratype 10	35.1	13.7	(Philippines)	*
Paratype 11	27.6	11.6	(Philippines)	MCZ 361609

(Continued)

APPENDIX
(Continued.)

	Length	Width	Locality (PI)	Depository (Cat#)
Paratype 12	28.3	12.5	(Philippines)	ANSP 421620
Paratype 13	36.6	15.0	(Philippines)	*
Paratype 14	35.8	14.7	Panglao Is.	BMSM 38673
Paratype 15	35.5	13.2	(Philippines)	*
Paratype 16	27.2	11.5	Aliguay	MNHN 21132
Paratype 17	26.9	11.5	Aliguay	*
Paratype 18 (Fig 2)	18.5	7.4	Aliguay	MSI
Paratype 19	25.5	11.4	Aliguay	*
Paratype 20	33.7	13.5	Aliguay	*
Paratype 21	32.5	13.6	Balicasag Is.	*
Paratype 22	15.8	6.4	Panglao Is.	*
Paratype 23	33.3	14.2	Minabe, Wakayama, Japan	*
Paratype 24	28.8	12.4	Olango Is.	*

Conus rizali, summary of type specimens

	Length	Width	Locality (PI)	Depository (Cat#)
Holotype (Figs 3, 6)	26.6	12.4	Philippines	MSI
Paratype I	36.3	14.0	Philippines	*
Paratype 2 (Figs 1, 3)	26.1	10.2	Philippines	MSI
Paratype 3	34.5	13.9	Philippines	*
Paratype 4	38.2	15.8	Philippines	ANSP 421621
Paratype 5	37.3	14.8	Philippines	MCZ 361610
Paratype 6	39.0	14.5	Philippines	MNHN 21133
Paratype 7	37.8	14.2	Philippines	*
Paratype 8	35.9	14.4	Balut Is.	*

Abbreviations: MSI, Marine Science Institute, University of the Philippines, Quezon City, Philippines, ANSP, Academy of Natural Sciences, Philadelphia, PA, USA; MNHN, Musćum national d'Histoire naturelle, Paris, France; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, MA, USA; BMSM, The Bailey-Matthews Shell Museum, Sanibel FL, USA; FMHN, Field Museum of Chicago, Chicago IL, USA; Lc, Zoological Museum of Moscow State University, Moscow, Russia; *, These specimens will be deposited in public museums, but have not yet been assigned.

An anatomical note on *Moellendorffia eastlakeana* (Möllendorff, 1882) a camaenid land snail from Vietnam (Gastropoda: Pulmonata: Camaenidae)

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ABSTRACT

Newly collected specimens of *Moellendorffia eastlakeana* (Möllendorff, 1882) expand the known range of this species into Vietnam. Using these new Vietnamese and existing museum samples we have re-described the species including new information on radula and genital anatomy. Comparison with the type material of *M. callitricha* (Bavay and Dautzenberg, 1899) from Vietnam suggested *M. callitricha* is a junior synonym of *M. eastlakeana*.

Additional keywords: Gastropoda, pulmonate, *Traumatophora*, *Chloritis*, *Trichelix*

INTRODUCTION

The land snail genus *Moellendorffia* Ancey, 1887, has a wide distribution in southeastern China, Hong Kong and Vietnam. The detached peristome, descending aperture with denticles, and hirsute shell with external furrows, confer a very distinctive morphology on the shells (Pilsbry, 1890, 1895, 1902, 1905; Yen, 1939; Azuma, 1982).

Currently, seven species are recognized within this genus, namely: *M. trisinuata* (von Martens, 1867), *M. eastlakeana* (Möllendorff, 1882), *M. hensaniensis* (Gredler, 1885), *M. loxotata* (Mabille, 1887), *M. messageri* (Bavay and Dautzenberg, 1899), *M. spurca* (Bavay and Dautzenberg, 1899), and *M. depressispira* (Bavay and Dautzenberg, 1908) (Pilsbry, 1905; Zilch, 1966; Richardson, 1985).

Originally, *Moellendorffia* was placed by Pilsbry (1890) in a section of *Helix* (*Stegodera*) Martens, 1876, then reclassified by Pilsbry (1894) as a subgenus of *Helicodonta* Férussac, 1819, and finally (Pilsbry, 1905) as a distinct southeastern Chinese and Indo-Chinese genus related to *Stegodera* and allied to *Chloritis* Beck, 1837. Likewise, *Trichelix* Ancey, 1887, was originally placed by Pilsbry (1905) along with *Moellendorffiella* Pilsbry, 1905, as subgenera within *Moellendorffia*, and *Traumatophora* Ancey, 1887, as a subgenus of *Stegodera*. Subsequently, Schileyko (2003) recognized *Trichelix* as a genus distinct from *Moellendorffia* and Zilch (1959) separated *Traumatophora* as a genus distinct from *Stegodera* on the basis of the possession of a dextral shell with apertural teeth.

The early descriptive work on *Mollendorffia* was restricted to shell morphology (e.g., Pfeiffer, 1862; Mabille, 1887; Bavay and Dautzenberg, 1899; 1908, Pilsbry, 1902; 1905). Subsequently, Habe (1957), Azuma (1982), and Schileyko (2003) provided some additional anatomical information for *M. trisinuata* and *Trichelix eucharista* (Pilsbry, 1902) (= *M. (Trichelix) eucharista*). In this article, we examine specimens of *M. eastlakeana* collected from a forest reserve in northern Vietnam and compare them to museum material originally collected from other locations.

MATERIALS AND METHODS

We examined three specimens of *M. eastlakeana* collected in May 1999 from the Huu Lien Nature Reserve, Lang Son Province, northeastern border of Vietnam, which are now deposited in the Chulalongkorn University, Museum of Zoology (CUMZ). Type and other materials were critically examined in the Senckenberg Museum, Frankfurt (SMF) and Muséum National d'Histoire Naturelle, Paris (MNHN). Terminology for soft anatomy follows that of Habe (1957) and Schileyko (2003). The terms "proximal" and "distal" refer to a position relative to the genital orifice. Methodology for whorl counts and shell measurements follow Kerney and Cameron (1979).

Abbreviations: **at,** atrium; **e,** epiphallus; **fl,** flagellum; **fo,** free oviduct; **gd,** gametolytic duct; **gs,** gametolytic

sac; **hw,** head wart; **ov,** oviduct; **p,** penis; **pp,** penial pilaster; **pr,** penial retractor muscle; **pv,** penial verge; **v,** vagina; **vd,** vas deferens; **vp,** vaginal pilaster.

SYSTEMATICS

Family Camaenidae

Genus *Moellendorffia* Ancey, 1887

Type species: *Helix trisinuata* von Martens, 1867, Hong-Kong, China; by subsequent designation of Pilsbry (1905: 64).

Diagnosis: Shell medium size (11.5×19.5 mm), depressed, rather thin, umbilicate and corneous to brownish. Spire low to slightly convex; embryonic shell nearly smooth; subsequent whorls granulated and with short to long periostracal hairs. Last whorl rounded to shoulder and suddenly descending anteriorly. Aperture trigonal or squarish, entirely free from preceding whorl; usually with barriers inside and externally marked with furrows. Peristome expanded and continuous. Penis and epiphallus long, flagellum short and vagina long. Penial wall with longitudinal pilasters. Radula with triangular-shaped teeth.

Moellendorffia eastlakeana (Möllendorff, 1882)

Helix eastlakeana Möllendorff, 1882: 185 (Tai-mo-shan, Kwangtung, China (= Hong Kong): Lectotype SMF 8328 by Yen, 1939); Möllendorff, 1885: 391, pl. 10, fig. 18. Ancey, 1887: 64

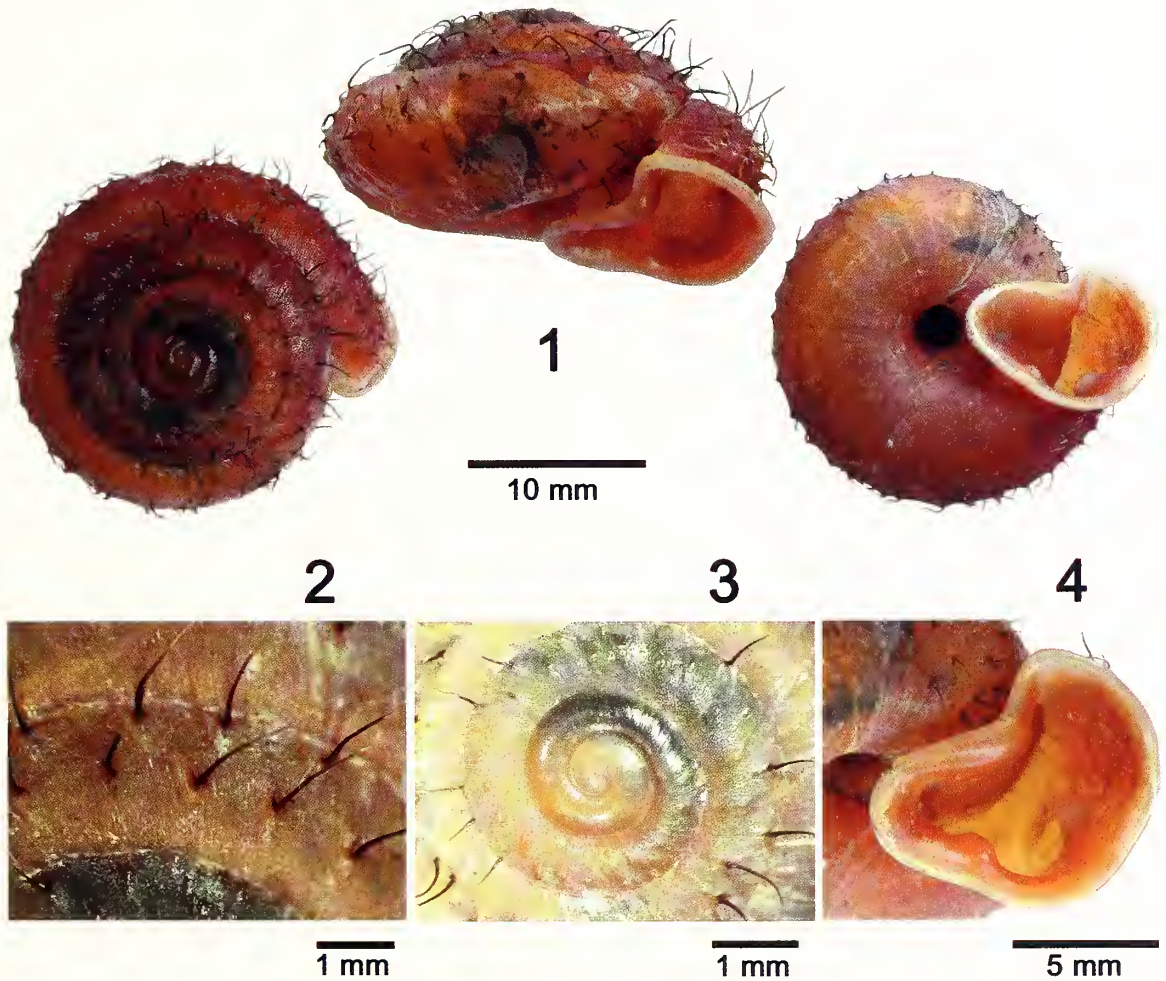
Helix (Moellendorffia) eastlakeana.—Pilsbry, 1890: 12, 13, pl. 1, figs 21, 22; Pilsbry, 1895: 290.

Stegodera eastlakeana.—Pilsbry, 1890: 310 (figure legend), pl. 1, figs 21, 22.

Helix (Moellendorffia) callitricha Bavay and Dautzenberg, 1899: 35, pl. 1, figs 6, 6[b] (That-Khé near Lang Son, Vietnam).

Moellendorffia eastlakeana.—Pilsbry, 1905: 65; Yen, 1939: 125, 228, pl. 13, fig. 3 (Lectotype SMF 8328); Richardson, 1985: 184.

Moellendorffia callitricha.—Pilsbry, 1905: 66; Richardson, 1985: 183.



Figures 1–4. Shell characteristics of *Moellendorffia eastlakeana*, CUMZ 2547. **1.** Shell morphology. **2.** Shell surface structure and showing the bristles on the periostracum. **3.** Protoconch sculpture **4.** Apertural lamellae.

Moellendorffia (Moellendorffia) eastlakeana.—Zilch, 1966: 210, pl. 6, fig. 52 (Lectotype SMF 8328).

Material Examined: Tai-mo-shan, Hong Kong: Lectotype SMF 8328, Paralectotype SMF 8329 (2 shells); Huu Lien Nature Reserve, Lang Son Province, Vietnam: CUMZ 2547 (1 specimen), CUMZ 2549 (2 shells); That-Khé, Tonkin, Vietnam (1 shell), MNHN Holotype of "*callitricha*"; That-Khé, Tonkin, Vietnam (2 shells), Denis collection (NMHN); That-Khé, Tonkin, Vietnam (1 shell), Staadt collection (NMHN); Tonkin, Vietnam (1 shell), Messager collection (NMHN); Tonkin, Vietnam (2 shells), Messager collection (NMHN)

Measurements: From 10 specimens analyzed; shell height ranged from 12.4 to 14.7 mm (mean 13.5±1.0 mm); shell width ranged from 20.8 to 23.9 mm (mean 22.0±1.2); and whorl count ranged from 6.0 to 6.1 whorls.

Shell: Shell (13.5 mm height, 22.0 mm width) slightly thin, translucent, depressed globose and deeply umbilicate. Spire flat to convex. Shell brownish to light brown; upper surface with long hairs (Figures 1, 2); lower surface with short hairs, few hairs around umbilicus. Shell surface rough, rows of tubercles running obliquely and descending, relatively smooth around umbilicus. Embryonic shell large and with very fine growth lines (Figure 3). Whorls 5-6, slightly convex and increasing regularly; suture depressed. Last whorl rounded and little convex below periphery. Aperture ear-shaped; lip margin light brown and continuously expanded; externally with furrows. Peristome free from preceding whorl and abruptly descending. Aperture brownish inside with well-developed, whitish, and semi-circular palatal and basal lamellae located closed to apertural lip. Two external furrows align with the internal apertural denticles. Parietal callus thickened, elevated, emarginated and obtusely projecting inward (Figure 4).

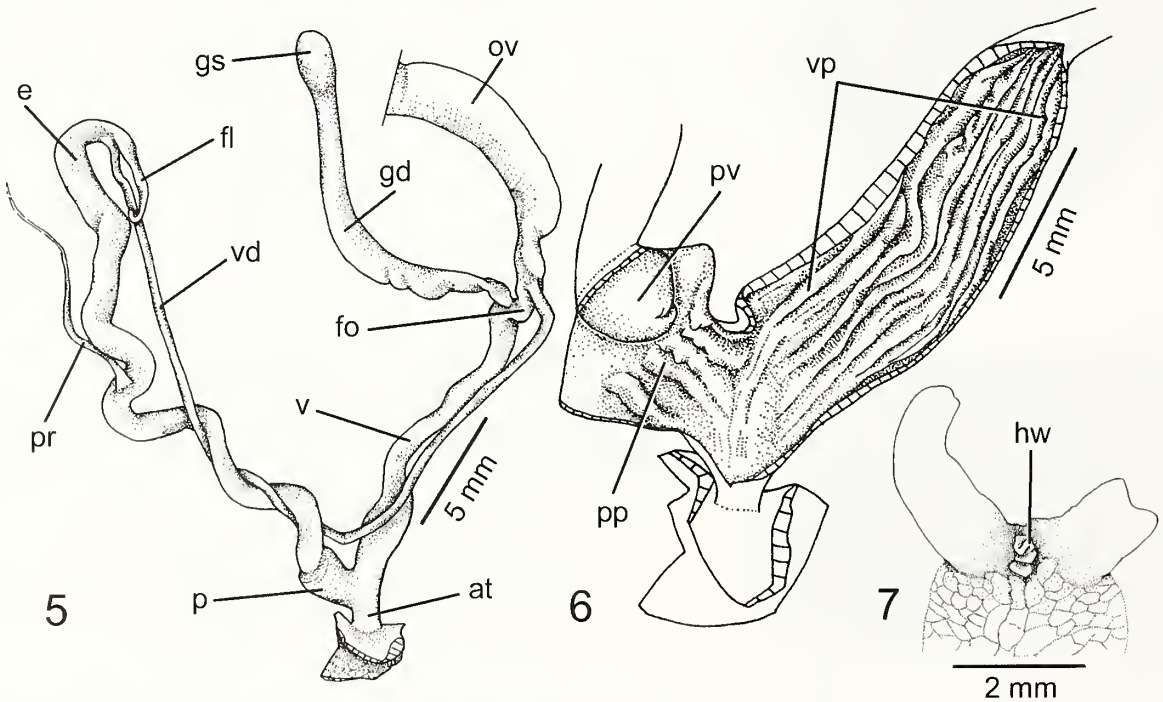
Genitalia: Atrium (**at**) short; penis (**p**) long; proximally with short penial verge and folded at penial verge based; distally long and somewhat slender. Epiphallus (**e**) shorter than penis. Flagellum (**fl**) short, small and without appendix. From free oviduct, vas deferens (**vd**) follows vagina and penis and connects distally on epiphallus. Penial retractor muscle (**pr**) thin and very long (Figure 5).

Internal wall of penis ribbed by series of swollen longitudinal pilasters (**pp**) (Figure 6). Smooth pilasters line introverted penial chamber and encircle penial verge tip. Penial verge (**pv**) short, conic and smooth (Figure 6).

Vagina (**v**) of similar length to penis, cylindrical and held in position by connective tissue attached to foot floor. Slightly swollen proximally; more slender distally. Gametolytic duct (**gd**) as wide as gametolytic sac (**gs**) for most of its length but narrows before gemetolytic sac. Free oviduct (**fo**) short; oviduct (**ov**) small (Figure 5).

Internal wall of vagina possess several longitudinal vaginal pilasters (**vp**) with smooth pilaster surfaces (Figure 6).

Animal: Live animal covered with blackish reticulated skin and dorsally with whitish stripe in middle of the



Figures 5–7. Reproductive system of *Moellendorffia eastlakeana*, CUMZ 2547. **5.** General view of the genital system. **6.** Interior structure of the atrium, penis and vaginal chamber. **7.** Dorsal view showing head wart.

body. A small curve-shaped head wart (**hw**) is loeated between the posterior tentacles (Figure 7). Foot narrow and long; mantle edge grayish; tentacles gray, and lower tentaeles paler. Mantle eavity with blackish pigmentation. Live snails possess short to long periostraeal hairs, whieh mostly break off after death.

Radula: Teeth arranged in anteriorly pointed V-shaped rows, eaeh row contains about 70 (34-(15-17)-1-(15-17)-35) teeth. Central tooth triangular with minute ectocones. Teeth beeome taller laterally. Lateral teeth tricuspid; endoeones and ectoeones small and located half way along tooth length (Figure 8). From tooth 16 to 17 outward lateral teeth, the marginal ectocone originates from the tooth base (Figure 9). Marginal teeth rather small, trieuspid and aligned obliquely; endocone becomes taller than mesocone; ectocone located basally (Figure 10), sometimes divided into two or three eusps in outermost teeth.

Distribution: *Moellendorffia eastlakeana* was previously known only from the type loeality: Tai-mo-shan, Hong Kong (Möllendorff, 1882, 1885; Pilsbry, 1890; Yen, 1939; Zileh, 1966). Our material was eollected from Huu Lien Nature Reserve, Lang Son Province, northeastern border of Vietnam.

Remarks: On examination of the holotype of *M. callitricha* and other topotypic material identified as this speeies, the only deteetable differenee was a slightly elevated spire relative to that of the lectotype of *M. eastlakeana* and other material recognized as *M. eastlakeana*. On this basis we consider *M. callitrieha* to be a junior synonym of *M. eastlakeana*.

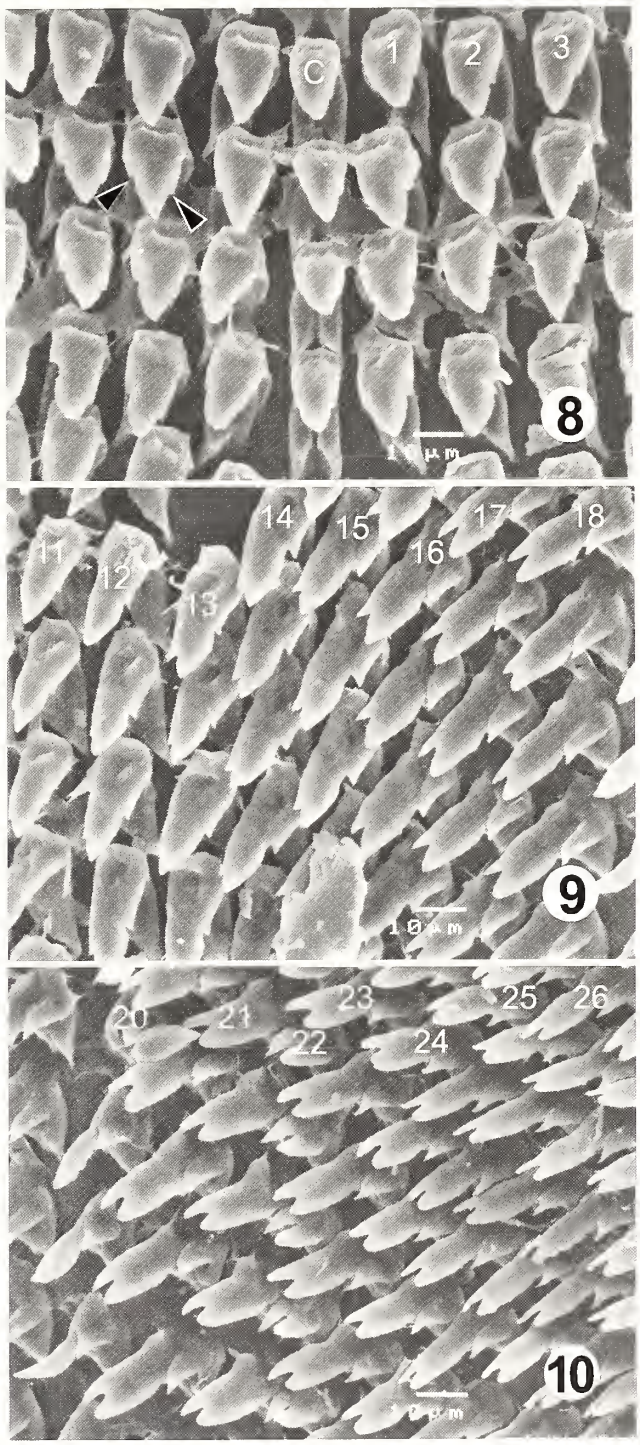
The locality characteristic of our sampling is monsoonal karst landform with high humidity. The snails oceurred among the tropical moist deeiduous forest. There was rain before the time of our visit in May, 1999. The snails were aetive, erawling on moist rotten logs.

Moellendorffia (M.) eastlakeana is distinctly different in shell morphology from *M. (M.) messageri* (Bavay and Dautzenberg, 1899), which occurs in the same area. The latter species has a much smaller shell (about 8 mm height; 14 mm width), flattened spire and shouldered last whorl.

DISCUSSION

The newly eolleeted material from Vietnam presents valuable additional information for the taxonomie revision of *Moellendorffia* and it allies. The presence of shell apertural lamellae and shell external furrows appear as eommon shell characters among *Moellendorffia*, *Trichelix*, and *Moellendorffiella*.

In eonsideration to the generie relationship, the presence of lamellae and external furrows could be common eharaeters among *Moellendorffia*, *Trichelix*, and *Moellendorffiella*. The long epiphallus, short flagellum, and triangular shape of the radula eentral tooth in both



Figures 8–10. Scanning electron micrographs of *Moellendorffia eastlakeana* radula, CUMZ 2547. **8.** Central teeth with the first to the third lateral teeth (black arrows indicate endocone and ectocone). **9.** Lateral teeth with the tricuspid marginal teeth transition. **10.** Marginal teeth. Central tooth is indicated by "C" and the other numbers indicate the order of lateral and marginal teeth.

Trichelix and *Moellendorffia* (Habe, 1957; Schileyko, 2003) may support their having a close relationship. The parietal callus free from a preceding whorl, with aperture lamellae, ear shaped aperture, and long hairs are possibly the distinctive characters of *Moellendorffia* sensu stricto. The position of two furrows (upper and lower periphery), parietal callus thickened at the edge, and tuberculated penial wall are probably the unique characteristics of *Trichelix*. Unfortunately, the anatomy of species of *Moellendorffiella* is still lacking for comparison, but the differences between shells of *Moellendorffiella* and *Moellendorffia* are the shouldered last whorl, flattened spire, parietal callus shortly attached to penultimate whorl, and rounded aperture (Pilsbry, 1890, 1905). These differences support the distinct generic position of *Moellendorffia*, *Trichelix*, and *Moellendorffiella* as proposed by Schileyko (2003). However, with so few samples and, especially, so few different species and informative morphological characters, the exact phylogenetic relationships remain equivocal. To better resolve the exact phylogeny, we suggest that the anatomical examination from more localities within each species range and from different species required is still insufficient, however a molecular based phylogenic approach is required in conjunction with morphology traits.

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Terrestrial gastropods from Haida Gwaii (Queen Charlotte Islands), British Columbia, Canada, including description of a new northern endemic slug (Gastropoda: Stylommatophora: Arionidae)

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ABSTRACT

Reflecting its isolation, geography, and glacial history, the Haida Gwaii archipelago (Queen Charlotte Islands, British Columbia) contains numerous endemic and disjunct taxa of various groups of organisms, but terrestrial gastropods have received scant attention. During surveys of 56 sites on Graham and Moresby Islands and 11 smaller islands, including remote mountain top locations, we detected 18 species of native terrestrial gastropods, most of which also occur in southwestern British Columbia. An undescribed species of semi-slug was found at four sites on Graham Island and six sites on Moresby Island and is formally described (Arionidae: *Staala gwaii*). Morphological and anatomical analyses suggest that the new slug is related to small species of *Hemphillia* Bland and Binney, 1872, but the differences are substantial, warranting the establishment of a new genus. The new species is of particular interest because it appears to be a northern endemic and a relict to the archipelago.

Additional keywords: Gastropoda, Arionidae, *Staala gwaii*, Queen Charlotte Islands, anatomy, endemism

INTRODUCTION

Haida Gwaii (Queen Charlotte Islands) is an isolated archipelago located at the edge of the North American continental shelf in the North Pacific Ocean. A distance of at least 80 km separates the islands from the nearest landmass to the east across Hecate Strait on the mainland British Columbia and to the north across Dixon Entrance on the Alaskan panhandle. The biota of the islands includes endemic and unusual disjunct populations from a wide range of taxonomic groups (e.g., vascular plants: Ogilvie, 1989, 1994; bryophytes: Schofield, 1989a,b; carabid beetles: Clarke et al., 2001; birds and mammals: McTaggart Cowan, 1989). Endemism and disjunct distributions have been interpreted to reflect the geographic isolation of the archipelago and differentiation *in situ*, in combination with complex patterns of past recolonization and extinction events.

Terrestrial gastropods of Haida Gwaii are poorly documented, and knowledge of this group is largely restricted to serendipitous observations as part of studies of other organisms. Terrestrial gastropods as a group can be useful for elucidating phylogeographic patterns, as many species have poor dispersal abilities if not aided by humans and can survive in small habitat patches (Cowie and Holland, 2006). From 2000 to 2004, we surveyed numerous sites on the two main islands (Graham and Moresby) and on smaller islands of the archipelago for terrestrial gastropods. Here we report the results of these surveys and describe a new genus and species of arionid semi-slug, presumed to be a relict, and endemic to the archipelago.

MATERIALS AND METHODS

Study Sites: We sampled 56 sites on Graham (6883 km^2) and Moresby (3066 km^2) islands and on 11 smaller islands in the Hecate Strait: Lyell (181 km^2), Kunghit (134 km^2), Burnaby (66 km^2), Tanu (23 km^2), Huxley (6.7 km^2), SGang Gwaii (2.9 km^2), Kat (0.7 km^2), Bischofs (1.1 km^2), Hotspring (0.2 km^2), Ellen (0.2 km^2), and Slug Islet (0.03 km^2) (Figure 1; see RBCM website for coordinates and habitat descriptions). More than one habitat or sub-site within a 1 km area was sampled at seven of these sites. The surveys took place in Apr. 2000, Jul.–Oct. 2002, Sep.–Nov. 2003, and Sep. 2004. The focus was on old-growth forest (28 sites), dominated by *Picea sitchensis*, *Tsuga heterophylla*, and *Thuja plicata* and with an understory of *Vaccinium* species, *Gaultheria shallon*, *Menziesia ferruginea*, and *Blechnum spicant*. Other habitats sampled consisted of older (> 80 years old) second-growth coniferous forest (12 sites), young forest with a large component of *Alnus rugosa* (< 60 years old) (3 sites), subalpine and alpine meadows (7 sites), bog

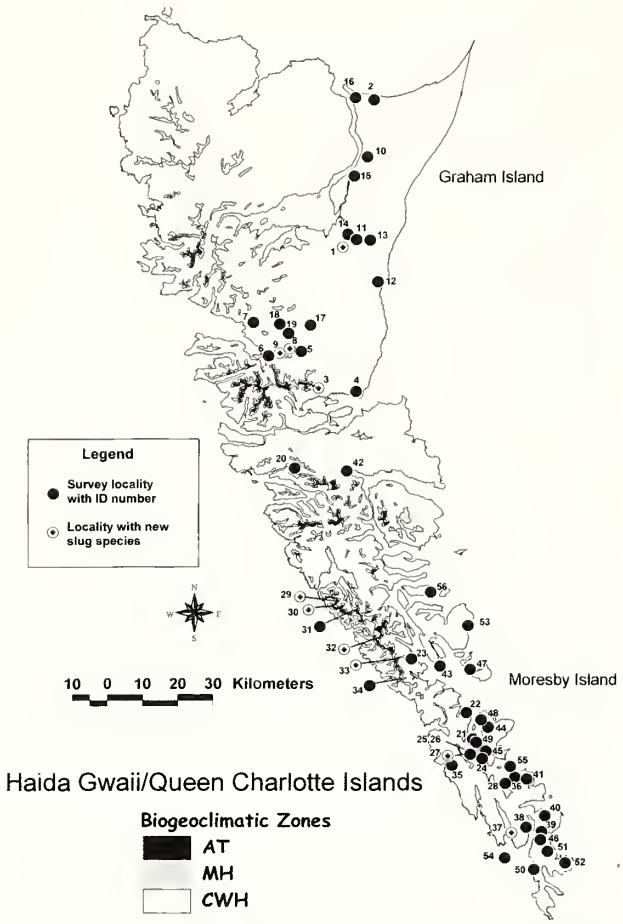


Figure 1. Map of sampling sites in the Haida Gwaii (Queen Charlotte Islands archipelago. Site numbers correspond to those in Table 1 (see RBCM website for coordinates and habitats). Biogeoclimatic zones: AT-alpine tundra, MH-mountain hemlock, CWH-coastal western hemlock (Meidinger and Pojar, 1991).

with stunted trees (3 sites), and other open habitats (rocky bluff, wet meadow, riparian fringe, thermal meadow, sand dune) (9 sites). The alpine sites were on rocky slopes with sparse ground cover, including hummocks of grasses, sedges, heathers, and crowberry (*Empetrum nigrum*). The subalpine sites contained scattered stunted trees and shrubs, including *Pinus contorta*, *Chamaecyparis nootkatensis*, *Tsuga mertensiana*, and *Juniperus* species. In 2004, we specifically targeted subalpine-alpine habitats, which were suspected to support populations of the new species of slug.

Gastropod Sampling and Identification: The main survey methods consisted of timed searches of natural cover on the forest floor (59 plots at 50 sites) and inspections of cardboard cover-objects (36 plots at 9 sites). Additionally, we extracted small snails from litter samples from two sites, including an experimental forestry site that was sampled intensively in two years (102 l of litter dried and sieved and residues examined for snail shells). Searches of natural cover focused on key microhabitat features for gastropods, such as piles of bark or an abundance of decaying logs or stumps. Observers visually scanned the surface of the forest floor and vegetation, turned over downed logs, sloughed-off bark, and rocks, and examined handfuls of leaf-litter. At one site (Site 2a–d in Figure 1), the surveys were both time- and area-constrained, and the observers searched 100×1 m transects in four different habitats for 40 minutes. The total search time for surveys of natural cover was 86.7 person-hours ($\bar{x} \pm SE = 88 \pm 7$ min/site).

The cardboard cover-object method (Hawkins et al., 1998) permitted repeated sampling of gastropods with minimal disturbance to the habitat. We used cover-objects constructed of layers of corrugated cardboard (dimensions 30 cm x 30 cm) placed at stations 10 m apart along transects of 10 sampling stations and inspected them one or more times after they had weathered on the forest floor for at least two weeks. There were a total of 1072 cardboard cover-objects on 36 plots at 9 sites. One site (Site 1 in Figure 1) was used as an experimental site for investigating logging effects and was sampled intensively and repeatedly (800 cover-objects inspected four times; in 2002 and 2006; KO and LS, unpublished data).

Identification of gastropods was based on descriptions in Pilsbry (1940, 1948) and Forsyth (2004). Nomenclature follows Forsyth (2004). Snails were identified using shell characteristics. Any small snails that could not be readily identified in the field were collected and examined under a dissecting microscope. Some snails (notably juveniles of *Ancotrema* and *Pristiloma*, and most *Vertigo*) were identified to genus only. Of slugs, several specimens of *Staala gwaii*, new species, and a sample of *Prophysaon foliolatum*, and *P. vanattae*, were dissected, and their reproductive anatomy was examined. Voucher specimens are deposited in the Royal British Columbia Museum, Victoria, British Columbia, Carnegie Museum of Natural History, and in the personal collections of K. Ovaska and R. Forsyth.

Dissection of Specimens: Seven specimens of the new species, preserved in 70% ethanol, were dissected by LC under a dissecting microscope (7.5–35X magnification). Parts removed for further study were mounted on standard microscope slides and examined under a compound microscope (40–400X magnification). Hematoxylin stain was used to make a permanent slide of the penis. Mounted specimens were dehydrated in 95% and 100% ethanol. Toluene was used as a clearing agent and specimens were mounted in Permount (Fisher Scientific, Fairlawn, New Jersey).

RESULTS

Gastropod Species Found

Surveys of 56 sites resulted in the detection of 18 native and four alien species of terrestrial gastropods (Table 1). Five species predominated in the samples: *Ariolimax columbianus* (71.4% of sites), *Vespericola columbianus*

Table 1. Species of terrestrial gastropods by locality found during surveys in Haida Gwaii (Queen Charlotte Islands) in 1999 – 2004. See Figure 1 for location of the sites, indicated by numbers (letters denote sub-sites).

Species	Graham Island (n = 19 sites)	Moresby Island (n = 23 sites)	Small outer islands (n = 14 sites on 11 islands)
Agriolimacidae:			
Deroceras laeve Müller, 1774	2a, 5, 17	26	
Deroceras reticulatum Müller, 1774*	2d		47b
Arionidae:			
Ariolimax columbianus Gould *in* A. Binney, 1851	1, 2b–d, 3a, 4, 5, 6, 7, 11, 12, 13, 14, 15, 16b, 17, 18	20, 21, 22, 24, 25, 27c, 28, 29, 30, 37, 38, 39, 40, 41, 42	43, 45a, 46, 47b, 48, 50, 53, 54a,b, 55, 56
Arion rufus Linnaeus, 1758*	2d, 4		
Arion subfuscus Draparnaud, 1805*	2d, 16a	36	
Prophysaon foliolatum Gould *in* A. Binney, 1851	1, 2a–d, 4, 5, 6, 7, 9, 12, 13, 14, 15, 16b, 17	23, 27c, 30, 31, 33, 34, 35, 36, 40, 41	43, 45b, 46, 47b, 48, 50, 51, 52, 53, 54a, 56
Prophysaon vanattae Pilsbry, 1948	1, 2b,c, 5, 12, 14	20, 29, 30, 37	48, 52
Staala gwaii (new genus and species)	1, 3a,d, 8, 9	27b,c, 29, 30, 32, 33, 37	
Daudebardiidae:			
Nesovitrea binneyana Morse, 1864	2d		47a
Oxychilus alliarius J.S. Miller 1822*	2d		
Euconulidae:			
Euconulus fulvus Műller, 1774	1		47a
Gastrodontidae:			
Striatura pugetensis Dall, 1895	1, 2a–c, 3a, 5, 6, 12, 13	28	
Haplotrematidae:			
Ancotrema hybridum Ancey, 1888	1, 2a		51, 54a
Ancotrema Baker, 1931 sp.	6, 7, 8	39	46, 48, 53
Haplotrema vancouverense, I. Lea, 1839	1, 2a–d, 3a, 4, 5, 7, 10, 12, 13, 15, 16b, 17	20, 21, 22, 23, 24, 25, 27b, 28, 29, 36, 37, 39, 40, 41, 42	43, 44, 45b, 46, 51, 52, 53, 54a, 55, 56
Punctidae:			
Punctum randolphii Dall, 1895	1, 2a–c, 5, 6, 12	21, 23, 25, 28, 37, 41	45a, 48, 49, 50, 51, 52
Pristilomatidae:			
Pristiloma lansingi Bland, 1875	1, 4, 5, 6, 17		
Pristiloma stearnsii Bland, 1875	1, 2b,c, 3a,b, 5, 8, 9, 10, 11, 12, 19	20, 21, 22, 23, 24, 25, 28, 29, 37, 39, 40, 41	43, 44, 46, 47b, 48, 49, 50, 51, 53, 54a,b
Pristiloma Ancey, 1887 sp.(subgenus *Pristiloma*)	1, 2b,c, 3a, 4, 5, 7, 9, 11, 12	22, 28, 37, 38, 39, 40, 41, 42	48, 49, 50, 51, 52, 54a
Polygyridae:			
Cryptomastix germana Gould *in* A. Binney, 1851	1, 17		
Vespericola columbianus I. Lea 1839	1, 2a–d, 3a, 4, 5, 6, 7, 9, 10, 12, 13, 15, 18, 19	20, 21, 22, 23, 24, 25, 26, 28, 37, 38, 39, 40, 41, 42	43, 44, 45a,b, 46, 47a,b, 49, 50, 51, 52, 53, 54a,b, 56
Vallonidae:			
Planogyra clappi Pilsbry, 1898	6, 12, 18	41	
Vertiginidae:			
Columella edentula Draparnaud, 1805^	1, 8	21, 28	
Vertigo columbiana Pilsbry *and* Vanatta, 1900	1, 2b,c, 5, 6	20, 23, 25, 28	43, 48, 54b
Vertigo Müller, 1774 sp.	1, 2b,d, 8, 12	21, 22, 41	47a, 49, 50, 51, 52, 54a

*Denotes introduced species of European origin

^*Columella simplex* by some authors, in reference to the North America form of the holarctic species

(71.4% of sites), *Prophysaon foliolatum* (60.7% of sites), *Haplotrema vancouverense* (66.1% of sites), and *Pristiloma stearnsii* (57.1% of sites). All these speeies were widely distributed in forests throughout the archipelago. Several snails with unusual, clear, transparent shells were found at one loeality on Graham Island (Site 1 in Figure 1), but were attributed to *Pristiloma stearnsii* based on other shell features.

We found 18 speeies of terrestrial gastropods on Graham Island and 15 on Moresby Island. On the smallest island sampled, a roeky bluff (Slug Islet), we found two species; on the remaining 10 small islands we found 4–9 species each ($\bar{x}$ = 6.4, SD = 1.6).

Alien gastropods, represented by four speeies, were found only at a few sites that were either disturbed and in early successional stages on Graham and Moresby Islands or received regular human visitation (Hotspring Island); older forest and small islands, apart from Hotspring Island, appeared to be free of alien species.

Slugs, represented by *P. foliolatum*, *P. vanattae*, and *S. gwaii*, dominated the gastropod fauna in the subalpine and alpine sites sampled, whereas other gastropods, including *A. columbianus*, *H. vancouverense*, and *P. stearnsii* were found infrequently and in very low numbers in these habitats; *A. columbianus* oeeurred only at sites with patehes of trees and shrubs. *P. foliolatum* was the only gastropod found at two alpine sites that were devoid of trees and shrubs (Sites 31 and 34 in Figure1).

A New Species of Arionid Slug

A slug that did not fit within the description of any known speeies was encountered at four sites on Graham Island and six sites on Moresby Island (Figure 2, 3). The localities were near Rennell Sound, south of Port Clements, and on Mt. Genevieve (Sleeping Beauty Massif) on Graham Island, and on Yatza Mountain, Mt. Oliver, Mt. De la Touehe, unnamed mountains near Sunday Inlet and Kostan Inlet, and in Louseoone Inlet on Moresby Island.

Superficially, the slug resembled *Hemphillia glandulosa* Bland and W.G. Binney, 1872, found on Vaneouver Island, British Columbia, and in Washington and Oregon, but detailed morphological and anatomical examination revealed substantial differenees, warranting the establishment of a new genus. Preliminary genetie analyses using mitochondrial markers also place the species apart from all known genera of arionid slugs in western North America (Clade C in Wilke, 2004: fig. 2).

Arionid genera native to the Pacific Northwest include *Zacoleus* Pilsbry, 1903, *Udosarx* Webb, 1954, *Prophysaon* Bland and W.G. Binney 1873, *Kootenaia* Leonard, Chichester and Bangh, 2003, and *Hemphillia* Bland and W.G. Binney 1872. Arionid genera share a ribbed jaw. The new slug possesses a jaw that is subdivided into sectors by evenly spaced, finely incised lines. We consider this jaw to be sufficiently similar to the jaws of other arionids to warrant the inclusion of the new species to this family. The new slug further differs from the first four genera by possessing a visceral cavity that is elevated into a hump and that fails to extend to the tip of the tail. It shares this charaeter with *Hemphillia* (jumping-slugs), the only other genus of native semi-slugs known from North America. It differs from *Hemphillia* by having a shell plate that is calcareous and eompletely covered by the mantle and by a pattern of papillae eovering the entire body. See Table 2 for comparisons of major features among western North American genera of arionids. A formal deseription of the new genus, *Staala*, and species, *S. gwaii*, follows.

Figures 2–3. *Staala gwaii*. **2.** Adult (17 mm in extended length) from near Port Clements, Graham Island (Type locality, Site 1 in Figure 1). **3.** Juvenile (2 mm in extended length) from near Port Clements, Graham Island (Type locality, Site 1 in Figure 1).

Staala new genus

Type Species: *Staala gwaii* new speeies (below).

Diagnosis: Distinet from any other known arionid genus externally by having viseera in a pronounced hump and shell covered by mantle, and internally by the eomplexity of the penial stimulatory apparatus (see description in the following speeies aecount) and by the presence of an atrial accessory sac.

Etymology: The generic name means "slug" in Haida language and honors the aboriginal heritage of the archipelago of Haida Gwaii (Queen Charlotte Islands).

Table 2. Comparison of external and internal characteristics of *Staala* (new genus) with those of five other genera of Arionidae native to western North America.

Charaeteristic	*Staala*	*Zacoleus*	*Udosarx*	*Prophysaon*	*Kootenaia*	*Hemphillia*
EXTERNAL:						
Shell eompletely covered by mantle	yes	yes	yes	yes	yes	no
Shell shape	convex	convex	eonvex	flat	convex	convex
Shell ealcareous	yes	yes	yes	yes	yes	no
Caudal mucus pore present	yes	no	no	no	no	yes
Caudal abseission line present	no	no	no	yes	no	no
Tail eompressed *and* dorsally keeled	no	yes	yes	no	no	yes
Viscera in pronounced hump	yes	no	no	no	no	yes
Fleshy "horn" or protuberanee on tail	yes	no	no	no	no	In many species
INTERNAL:						
Penis reduced to a penial loop	no	no	no	yes	yes	no
Distinct epiphallus present	yes	yes	yes	yes	no	yes
Buceal *and* tentacular retractors eonverge	yes*	yes	yes	no	no	yes
Penial retraetor present	yes	no	yes	no	yes	yes

*Except the main braneh of the left tentacular retractor, which originates on the floor of the body cavity.

Staala gwaii new species

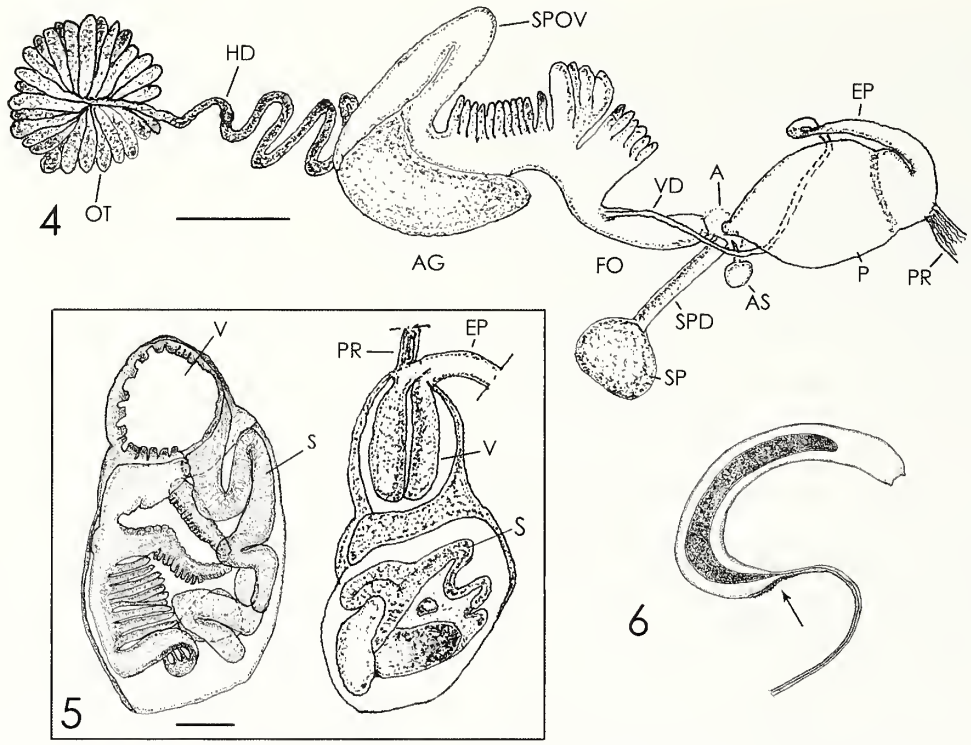
Description: SIZE: Very small; length of 16 live speeimens was 2–17 mm ($\bar{x}$ = 9.8 mm, SD = 5.7 mm) when extended in movement. Length of 12 preserved specimens was 3–11 mm ($\bar{x}$ = 8.1 mm, SD = 2.7 mm); the difference in size between live and preserved specimens probably refleets preservation techniques (live animals were maximally extended whereas the preservative, ethanol, resulted in shrinkage). Holotype: 16 mm live, 9.4 mm preserved. Smallest dissected and preserved individuals with a mature reproductive system were 8 mm in length.

EXTERNAL ANATOMY: The following deseription is based on examination of 40 individuals from ten sites and apply to the holotype, unless otherwise mentioned. Shell domeshaped and completely eovered by mantle. Outer layer horny and thin, and covering the entire viseeral hump; inner layer calcareous, thiekest at the center of the dome and largely absent at the margins. Mantle elliptieal and large, about 2/3 the length of the body and covering the visceral pouch, whieh is elevated into a pronounced hump; mantle hump flattened dorsally towards its distal end and ean be slightly asymmetrical, giving it a misshapen appearanee. Pneumostome slightly anterior or in the middle of the right side of the mantle, near mantle margin. Tail rounded dorsally, no keel evident; tail flattened and depressed at its base where the distal portion of the mantle rests. Several elevated lines of papillae and associated grooves radiate outwards from the depression. Tail protrudes distally over foot. Caudal mucus pore present. Head, mantle, and tail covered with numerous papillae. Foot fringe moderately wide; sole undivided.

COLOR: Head and base of tentaeles dark grey, sometimes bluish; tentacles lighter grey towards tips. Mantle mottled with dark grey and light grey (as in holotype) or tan, sometimes flecked with small tan specks. Dorsal surface of head and tail dark grey. Foot fringe light grey or tan, lighter than sides, sometimes with indistinct dark, vertical lines. Underside of head similarly light grey or tan. Black-tipped papillae often form dotted line at foot margin. Sole light grey or tan, dark grey in some melanistic individuals. Papillae covering head, mantle, and tail are light grey and black-tipped. Individuals from some localities, especially subalpine habitats on Moresby Island, were melanistic and almost uniformily dark with the exception of the sole that is slightly lighter.

Internal Anatomy: REPRODUCTIVE SYSTEM: The ovotestis comprises a large number of lobules (more than three dozen). It is partially embedded on the right posterior of the digestive gland. The exposed portion is lightly to moderately pigmented with black flecks. The hermaphroditic duct is long, slender, and straight in immature individuals and swollen and highly convoluted in sexually mature animals. The albumen gland is adherent to the spermoviduct (common duct). In sexually mature individuals both the albumen gland and the spermoviduct become greatly enlarged and the latter becomes strueturally more elaborate. In most individuals the spermathecal duct and free oviduct enter the shallow atrium separately. In two sexually immature individuals the two duets joined just before entering the atrium. The spermatheca (seminal receptacle or bursa copulatrix) is conical to ovoidal in shape; its duct is slender and tapered. In one specimen containing a single spermatophore, the spermatheca was forced into a fusiform shape and its duct into a corkscrew. The vas deferens arises as a slender duct from the spermoviduct, which also gives rise to the free oviduct. The vas deferens becomes even more slender as it curves aromnd the base of the penis at the penial junction with the atrium, only to thicken again as it transitions along the side of the penis eventually to become a greatly thickened epiphallus (Figure 4).

The epiphallus enters the penis at its apex. Inserted at the apex, at this epiphallus-penis junction, is the penis



Figures 4–6. Reproductive anatomy of *Staala gwaii* (specimen from type locality). **4.** Reproductive system. **5.** Bisected penis of two specimens of *Staala gwaii* from the type locality. Left: upper verge chamber (empty) and lower stimulatory chamber with its complex folds and lobes. Scale bar = 0.2 mm; Right: bisected verge in the upper chamber and a portion of the stimulator in the lower chamber. **6.** Spermatophore (ca. 2 mm in length) showing the denticle region (arrow). Terminal portion of the filament is missing. Abbreviations: **A,** atrium; **AG,** albumen gland; **AS,** accessory sac; **EP,** epiphallus; **FO,** free oviduct; **HD,** hermaphroditic duct; **OT,** ovotestis; **P,** penis; **PR,** penis retractor muscle; **SP,** spermatheca (bursa copulatrix); **S,** stimulator; **SPD,** spermathecal duct; **SPOV,** spermoviduct; **V,** verge; **VD,** vas deferens.

retractor musele, which is a wide band that passes directly back to its origin near the midline of the diaphragm. The penis is a large barrel-shaped strueture divided internally into an upper verge ehamber and a lower stimulator chamber (Figures 4, 5). A lightly pigmented band on the penis surface roughly corresponds to the boundary between the two inner chambers. The verge chamber contains a large conical structure we believe functions as a verge. The lumen of the epiphallus eontinues within the verge as a narrow passage that opens at or near the apex of the cone. The lower stimulator chamber is almost completely filled with a variety of attachments on the inner penial wall. Some are plumose while others are smooth-margined and lobed. In other slug species such structures have been referred to as stimulators and we extend that tradition in this case, although we have not been able to observe copulation to determine how this complex is employed. The penis enters the atrium independent of the spermathecal duct and the free oviduct. There is no accessory penial sac. However, there is a small atrial accessory sac present. This sae has a very slender duct, which enters the atrium independent of the other ducts. In immature individuals the sac is very small and difficult to see. A single spermatophore was found intact in one specimen. The spermatophore consists of a crescent-shaped main body and a long threadlike terminus (Figure 6). Near the junction of the two parts the surfaee bears a number of tiny denticles. The overall length of the spermatophore is about 2 mm.

Buccal and Tentacular Retractor Muscles: The left and right buccal retractor muscles fuse just posterior of the buccal mass. The fused band passes directly back to the origin near the midline of the diaphragm. The right tentacular retractor muscle passes between the male and female components of the reproductive system to its origin near the midline of the diaphragm. The left tentaeular retraetor musele is split into a main branch that originates from the floor of the body eavity on the left side. The other branch is very slender, almost nerve-like. This branch extends baekward toward an origin near the midline of the diaphragm thus preserving an overall pattern one might deseribe as eonverging. This pattern is disrupted only by the anomalous braneh of the left tentacular retractor. We did not find a retensor muscle.

Digestive System: The jaw bears fine, evenly spaced incised lines but is not ribbed. The radula is of the usual arionid type, with the central row of teeth tricuspid, the inner lateral rows bicuspid and the outer rows

tending toward elongation of the mesocones and reduction of the ectocones. The crop is large but otherwise unremarkable. The short, slender intestine makes three looping turns before arriving at the anal pore.

Holotype: From type locality, on cardboard cover-objects used to sample gastropods in a coniferous stand of mixed old-growth and naturally regenerated mature second-growth forest at elevation of 65–80 m; collected by J. Gray, L. Hyatt, C. Engelstoft, 7 Oct. 2002, Royal British Columbia Museum, RBCM 009-00035-001.

Paratypes: (1) Near summit of Mt. Genevieve, Graham Island (53°33.9′ N, 132°5.6′ W), from cardboard cover-objects in alpine meadow at elevation of about 800 m; collected by Luke Hyatt, 16 Oct. 2002, RBCM 009-00036-001; (2) mid-slope of Mt. Genevieve (Sleeping Beauty Trail; 53°15.8′ N, 132°12.9′ W), from cardboard cover-objects in old-growth coniferous forest at elevation of 340 m, collected by Kristiina Ovaska, Lennart Sopuck, and Berry Wijdeven, 22 Sep. 2004, Carnegie Museum of Natural History, CM97971 and RBCM 009-00038-001.

Type Locality: 13 km southeast of Port Clements, Graham Island (53°34.6′ N, 132°6.6′ W), Queen Charlotte Islands, British Columbia, Canada; a coniferous stand of mixed old-growth and naturally regenerated mature second-growth forest at elevation of 65–80 m.

Other Material Examined: Collected from Moresby Island by Kristiina Ovaska and Lennart Sopuck from under rocks or within krummholtz hummocks in subalpine meadows: (1) Yatza Mountain (52°21.5′ N, 131°26.0′ W), elevation 170–210 m, 14 Sep. 2003, RBCM 009-00037-001; (2) Mt. Oliver (52°42.9′ N, 132°1.4′ W), elevation 650 m, 14 Sep. 2004, RBCM 009-00039-001; (3) unnamed mountain near Kostan Inlet (52°34.7′ N, 131°44.0′ W), elevation 280 m, 14 Sep. 2004, RBCM 009-00041-001; (4) unnamed mountain near Sunday Inlet (52°37.9′ N, 131°50.4′ W), elevation 475 m, 14 Sep. 2004, RBCM 009-00040-001; (5) from within leaf litter along bank of small stream in old-growth coniferous forest: Louscoone Inlet (52°10.0′ N, 131°12.7′ W), elevation < 50 m, 17 Sep. 2004; RBCM 009-00042-001.

Etymology: The specific name (used as a name in apposition) *gwaii* means "island" or "home" in the Haida language and refers to the archipelago the slugs inhabit.

Natural History: The ten sites where the species was found ranged from lowland coniferous forest, dominated by Sitka spruce (*Picea sitchensis*), western redcedar (*Thuja plicata*), and western hemlock (*Tsuga heterophylla*), to subalpine tundra. The species was seldom found in lowland forest (2 sites), although most extensive search effort was in this habitat. It was more frequently encountered at mid-elevation forest containing yellow cedar (*Chamaecyparis nootkatensis*), mountain hemlock (*Tsuga mertensiana*), and/or shore pine (*Pinus contorta*), and in subalpine meadows and mountain slopes. The subalpine habitats were very moist with scattered, stunted (< 2 m tall) trees and bushes (*P. contorta*, *C. nootkatensis*, *T. mertensiana*, and *Juniperus* sp.) and swales of grasses, heather, and crowberry (*Empetrum nigrum*). In these habitats, we found slugs under rocks or within hummocks of ground vegetation. At the forested sites, we located the species by using cardboard cover-objects (see Methods); only one individual was found during visual searches of the forest floor. We found the smallest juveniles, about 2 mm in extended length, on 27–28 Jul. and 26 Sep. 2002 at a lowland site (Site 1 in Figure 1). We found larger juveniles and adult-sized individuals (> 10 mm in extended length) from September to November, 2002–2004. Longevity and life stages at which the slugs survive winter are unknown.

Possible Taxonomic Relationships: Of the previously described species, the new species most closely resembles small species of *Hemphillia* (*H. glandulosa*/*H. burringtoni* species complex). It differs from them externally by a mantle that completely covers the shell plate, which in the new species is calcareous, by dense, pointed papillae that cover the sides and the tail as well as the mantle, and by an unkeeled tail, and internally by an unusual configuration of buccal and tentacular retractors (Table 2).

DISCUSSION

The terrestrial gastropod fauna of Haida Gwaii is depauperate when compared to more southern areas along the Pacific coast, probably reflecting the isolation and harsh, northern climate of the archipelago; 18 native species were detected in contrast to over 35 species on Vancouver Island (Forsyth, 2004). With the notable exception of the new slug, *Staala gwaii*, all species of gastropods found during the surveys also occur on Vancouver Island and the coastal mainland of southern British Columbia. However, systematic relationships of some groups such as *Prophysaon*, *Pristiloma*, and *Vertigo* from western North America have not been examined recently, and genetic or detailed morphological studies could reveal differences among populations from Haida Gwaii and farther south. In particular, the unusual, clear-shelled *Pristiloma*, attributed herein to *P. stearnsii*, requires further investigation.

Curiously, we detected only infrequently two species that are relatively common on Vancouver Island and the lower mainland of British Columbia, *Nesovitrea binneyana* and *Euconulus fulvus*. Both snails were present in thermal meadows on Hotspring Island; *N. binneyana* also occupied sand dune habitat near Masset, Graham Island. We encountered *Cryptomastix germana* at only two sites within pockets of dense riparian herbaceous vegetation. This species has been reported previously from one Moresby Island locality (Forsyth, 2000). Some species (*Planogyra clappi*, *Cryptomastix germana*) probably exist at or near their northern limits of distribution in Haida Gwaii.

The new species of slug is of particular interest because it is possibly a relic of an ancient lineage that has survived several periods of glaciation on the archipelago. Ice-free refugia existed in various locations along the North Pacific coast from the Aleutian Islands to Vancouver Island during Pleistocene glaciations, and such refugia could have permitted the persistence of this and other endemic and disjunct species known from the islands through this and earlier glacial episodes. Paleoecological evidence exists for lowland ice-free refugia in Haida Gwaii at the height of the Wisconsin glacial epoch (Warner et al., 1982), but a continuous record of micro- or macro-fossils through this period is lacking. Some mountain tops in the Queen Charlotte Range are also thought to have remained as ice-free nunataks throughout glacial periods (Heusser, 1989) and probably supported organisms such as bryophytes (Schofield, 1989a) that are able to exist in small microhabitats and withstand harsh conditions. The slug could conceivably also have persisted in nunataks, as it is presently found in isolated mountain top habitats.

Some endemics on the archipelago appear to be of relatively recent origin as a result of rapid morphological evolution in post-glacial times within the past 15,000–16,000 years (e.g., carabid beetles of the genus *Nebria*: Clarke et al., 2001; Haida Gwaii black bear, *Ursus americanus carlottae*: Byun et al., 1997), whereas others are thought to be much older. Ancient, possibly Tertiary origins have been postulated for relic species of bryophytes that show unusual, disjunct distribution patterns (Schofield, 1989a).

Preliminary molecular analyses suggest that the lineage containing *Staala gwaii* is old and has split from *Hemphillia*, the presumed sister taxon, several million years ago (Wilke, 2004; Thomas Wilke, Animal Ecology & Systematics, Justus Liebig University Giessen, Giessen, Germany, pers. comm.), lending support to the notion that the slugs survived several glacial periods in refugia on the islands or elsewhere along the northwest coast of North America. Several species of plants endemic to the northwest coast have scattered and disjunct distributions (Calder and Taylor, 1968; Taylor, 1989; Ogilvie, 1989). Examples of endemic plants that co-occur with the slug in subalpine habitats in Haida Gwaii include *Geum schofieldii*, *Ligusticum calderi*, *Saxifraxa taylori*, and *Senecio moresbiensis* on Mt. De la Touche; *Ligusticum calderi* and *Saxifraga taylori* on Mt. Yatza; *Ligusticum calderi* on Mt. Oliver; *Saxifraga taylori* and *Senecio moresbiensis* on an unnamed mountain east of Blue Heron Bay (plant distribution from unpublished data files by Parks Canada).

Further surveys along the northwest coast of mainland British Columbia are needed to document the extent of the distribution of *Staala gwaii* and to explore the existence of other undiscovered species and populations. Comparative studies with other western North American and northeast Asian forms are also desirable, as they have potential to shed light on the evolution and biogeography of western North American slugs.

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How the number of hinge teeth may induce errors in the taxonomy of Nuculidae and Nuculanidae (Bivalvia)

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ABSTRACT

The hinge figures as an important feature in the taxonomy of bivalves, especially when soft parts are not available. For the Protobranchia, in addition to other shell features, the number of hinge teeth is often used in taxonomic studies. However, despite the importance of the number of hinge teeth, this character is not informative when shell size measurements are not available, since the number of teeth can increase during ontogeny. In addition, intraspecific variation may be observed for the same shell-size class. Since this variation has been up to now only empirically observed, the present study provides a statistical approach to the problem by computing the linear regression between number of teeth and shell size in 310 valves from five protobranch species (family Nuculidae: *Pronucula benguelana*; *Nucula semiornata*; *Ennucula puelcha*; and family Nuculanidae: *Adrana electa*; *A. patagonica*.) All species showed a statistically significant relationship (P value < 0.0001) between these characters.

Additional Keywords: Linear regression, shell morphology, Nuculoidea, Nuculanoidea, Protobranchia, taxonomy

INTRODUCTION

The protobranchs are a dominant bivalve group at abyssal depths, encompassing a high percentage of the bivalve species found in the deep-sea (Sanders and Allen, 1973). The recent sampling of deep-sea benthic fauna and the efforts of many investigators (e.g. Allen and Sanders, 1973, 1996; Moore, 1977; Rhind and Allen, 1992; Kilburn, 1994, 1999; Gofas and Salas, 1996; Roy et al., 2000; Allen, 2008; La Perna, 2008) have increased the number of known species and enlarged the known ranges of many protobranchs, providing a source for different proposals of classification for the group (e.g. Poel, 1955; Purchon, 1959; Cox, 1960; McAlester, 1964; Newell, 1969; Verril and Bush, 1897; Yonge, 1959; Sanders and Allen, 1973; Scarlato and Starobogatov, 1985; Allen and Hannah, 1986; Maxwell, 1988; Morton, 1996; Salvini-Plawen and Steiner, 1996; Coan, Scott, and Bernard, 2000; Schneider, 2001; Giribet and Wheeler, 2002; Giribet, 2008).

Among the protobranchs, the Nuculoidea Gray, 1824, and Nuculanoidea Adams and Adams, 1858, have had a problematic taxonomic history, often with obscure rearrangements of species and unclear changes in the higher-level taxonomy of many names (for more details see Schenck, 1934; Poel, 1955; Allen and Hannah, 1986; Maxwell, 1988; Rhind and Allen, 1992; Zardus, 2002). Most of the difficulties involved in the classification of the group arise from the conservative nature of the shell shape (Allen and Hannah, 1986) and from the morphological approach, which often considers only a single set of features (Sanders and Allen, 1973).

Although several characters have been taken into account (e.g., general outline, ornamentation and microstructure of the shell), in most taxonomic descriptions of protobranchs the hinge usually is an important taxonomic feature, especially when the studied specimens lack soft parts. The shape, number, position, and spacing of the teeth are often used in the diagnoses of species and even genera (Dall, 1886; Gofas and Salas, 1996). Moreover, the differences between the number of anterior and posterior teeth are used in identification, and even differences in the order of two or three teeth have been considered significant in descriptions or identification works (e.g. Esteves, 1984; Smith, 1885; Abbott, 1974; Kilburn, 1994; Rios, 1994; Espinosa and Ortea, 2001).

However, to consider the number of teeth without associating the character to measurements of shell size is not informative, and may cause taxonomic confusion. A morphometrical approach may improve on the traditional taxonomic methods and has been used with success by several authors (Bonfitto and Sabelli, 1995; Gofas and Salas, 1996; Fuiman et al., 1999).

This paper discusses the taxonomic importance of the size of the shell in proportion to the number of teeth on the hinge in three species of Nuculidae: *Pronucula benguelana* Clarke, 1961; *Nucula semiornata* d'Orbigny,

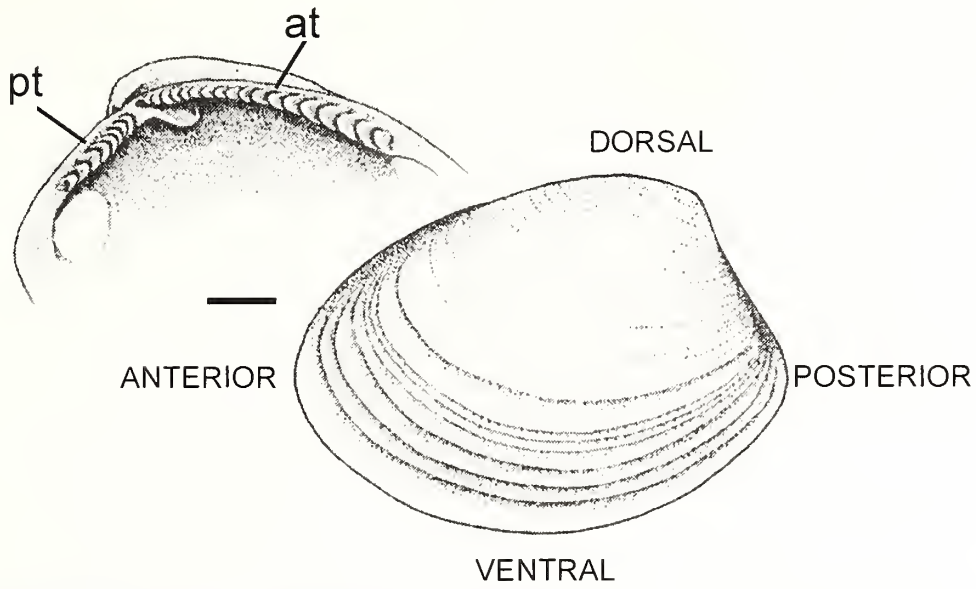


Figure 1. *Ennucula puelcha* d'Orbigny, 1842. Shell and the anterior and posterior hinge teeth. Abbreviations: at = anterior teeth; pt = posterior teeth. Scale bar = 2 mm. Adapted from Absalão & Pimenta (2005).

1846; *Ennucula puelcha* d'Orbigny, 1842; and two of Nuculanidae: *Adrana electa* (A. Adams, 1846); and *Adrana patagonica* (d'Orbigny, 1846).

MATERIALS AND METHODS

The material examined includes samples taken during different cruises undertaken the South Atlantic Ocean.

The measurements used herein are commonly used in morphometric studies with bivalves (Sibaja and Vilalobos, 1986; Bonfitto and Sabelli, 1995; Gofas and Salas, 1996; Fuiman et al., 1999), and are represented in Figure 1. The numbers of anterior and posterior teeth were counted with the aid of a ZEISS SV-6 stereoscopic microscope. The antero-posterior and dorso-ventral axes of each valve were measured using a caliper of 0.05 mm accuracy. A total of 200 valves of nuculids and 110 valves of nuculanids were considered in this study (Table 1). The statistical approach consisted of linear regression analysis (Sokal and Rohlf, 1981). All material from this study is deposited in the Mollusca collection of the Departamento de Zoologia, Instituto de Biologia, Universidade Federal do Rio de Janeiro (IBUFRJ).

Table 1. Descriptive statistics of the material analyzed. Abbreviation: sd = Standard deviation.

Species names	Antero-posterior axis	Dorso-ventral axis	Anterior teeth	Posterior teeth
Pronucula benguelana (N = 23)				
Range	1.7–3.8mm	1.6–3.45mm	5–10	3–7
Mean	2.81	2.62	7.65	5.52
sd	0.55	0.50	1.27	1.20
Nucula semiornata (N = 82)				
Range	0.85–6.85mm	1.0–6.8mm	6–23	2–10
Mean	3.60	3.43	13.93	5.76
Sd	1.72	1.71	4.70	2.09
Ennucula puelcha (N = 95)				
Range	1.65–15.25mm	1.55–13.65mm	4–22	2–9
Mean	6.71	6.20	13.24	5.25
sd	3.73	3.42	4.75	1.86
Adrana electa (N = 55)				
Range	12.45–56–60mm	3.20–14.55mm	32–64	31–71
Mean	35.68	9.15	50.76	55.47
Sd	9.20	2.66	7.11	10.02
Adrana patagonica (N = 55)				
Range	5–33.3mm	1.9–9mm	16–55	19–52
Mean	17.39	5.37	31.40	33.98
sd	6.22	1.88	6.68	5.91

Table 2. Results of statistieal analyses. Abbreviations: ap = antero-posterior axis; dv = dorso-ventral axis; at = anterior teeth; pt = posterior teeth.

Speeies names	x(ap) - y(at)	x(ap) - y(pt)	x(dv) - y(at)	x(dv) - y(pt)
P. benguelana	y = 1.798x + 2.597 R^2 = 0.607 F = 32.44 P value < 0.0001	Y = 1.68x + 0.793 R^2 = 0.589 F = 30.10 P value < 0.0001	y = 1.848x + 2.810 R^2 = 0.538 F = 24.49 P value < 0.0001	Y = 1.742x + 0.959 R^2 = 0.530 F = 23.72 P value < 0.0001
N. semiornata	y = 2.550x + 4.757 R^2 = 0.8707 F = 538.9 P value < 0.0001	Y = 1.139x + 1.659 R^2 = 0.8811 F = 592.7 P value < 0.0001	y = 2.555x + 5.152 R^2 = 0.8635 F = 506.1 P value < 0.0001	Y = 1.139x + 1.845 R^2 = 0.8693 F = 532.0 P value < 0.0001
E. puelcha	y = 1.152x + 5.514 R^2 = 0.8183 F = 418.8 P value < 0.0001	Y = 0.4425x + 2.284 R^2 = 0.7892 F = 348.1 P value < 0.0001	y = 1.266x + 5.396 R^2 = 0.8338 F = 466.5 P value < 0.0001	Y = 0.4858x + 2.241 R^2 = 0.8031 F = 379.3 P value < 0.0001
A. electa	y = 0.6188x + 28.68 R^2 = 0.6412 F = 94.73 P value < 0.0001	Y = 0.9373x + 22.03 R^2 = 0.7418 F = 152.3 P value < 0.0001	y = 1.953x + 32.90 R^2 = 0.5324 F = 60.34 P value < 0.0001	Y = 3.093x + 27.19 R^2 = 0.6732 F = 109.2 P value < 0.0001
A. patagonica	y = 1.006x + 13.90 R^2 = 0.8776 F = 380.1 P value < 0.0001	Y = 0.8626x + 18.98 R^2 = 0.8228 F = 246.1 P value < 0.0001	y = 3.205x + 14.18 R^2 = 0.8115 F = 228.2 P value < 0.0001	Y = 2.685x + 19.56 R^2 = 0.7261 F = 140.5 P value < 0.0001

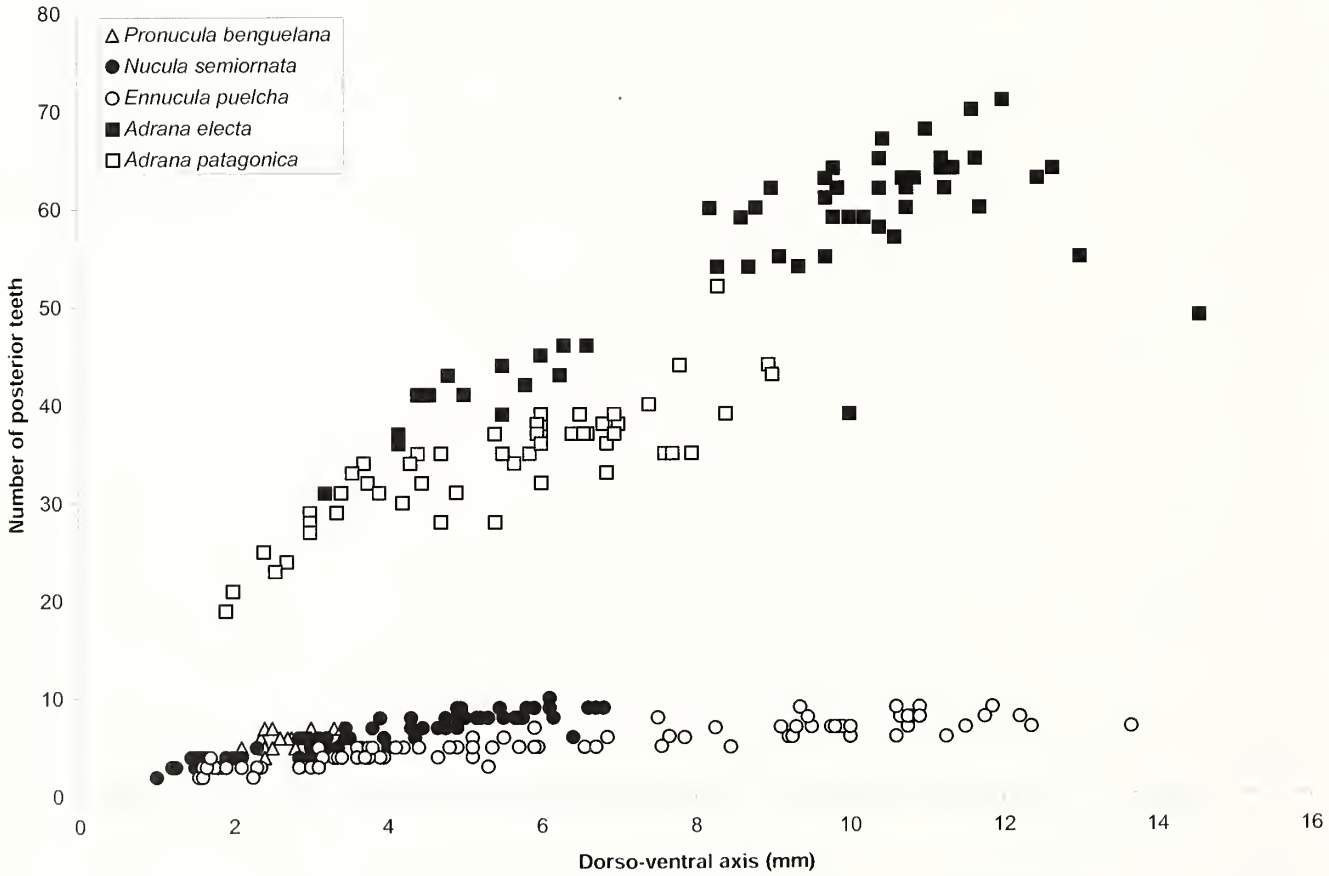
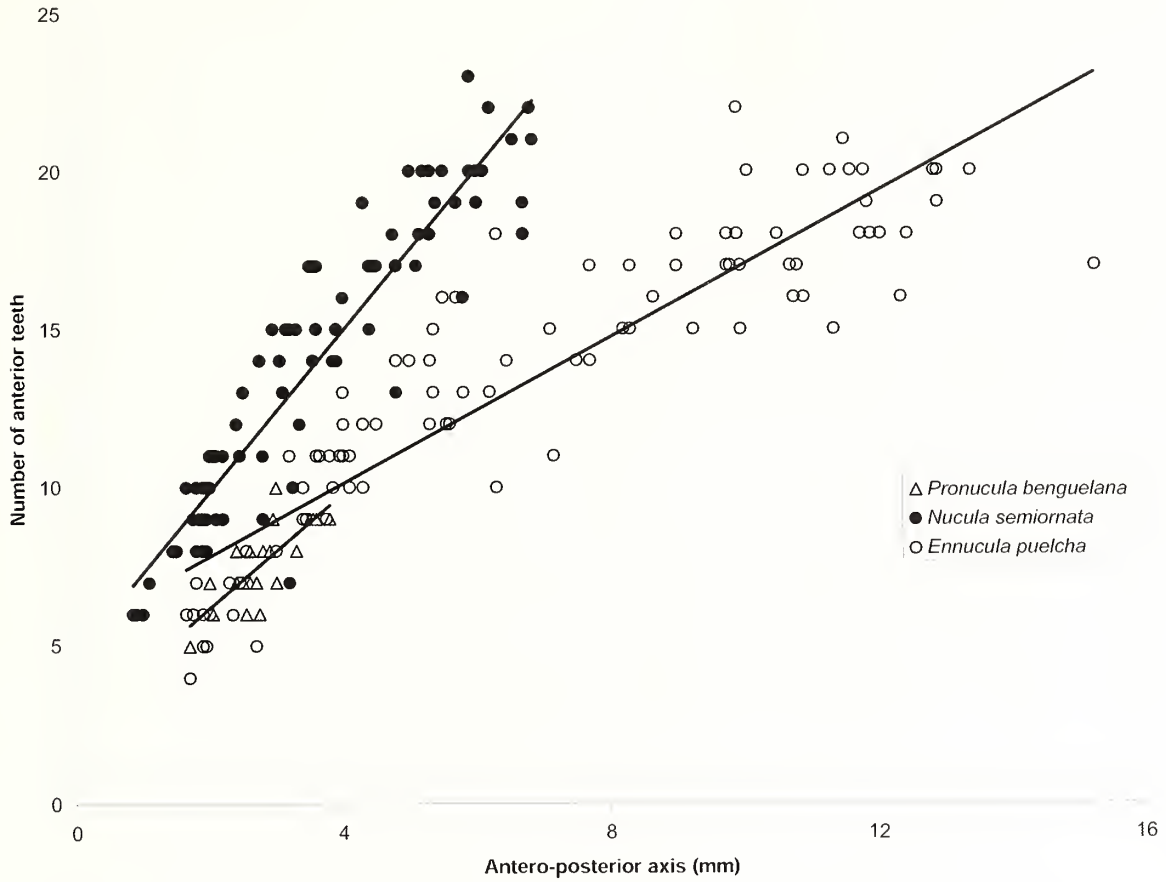


Figure 2. Relationship of dorso-ventral axis and number of posterior teeth in studied protobranch species. The two families analyzed occupy discrete morphospaces, reinforcing the importance of the number of teeth as a character at supra-specific levels.



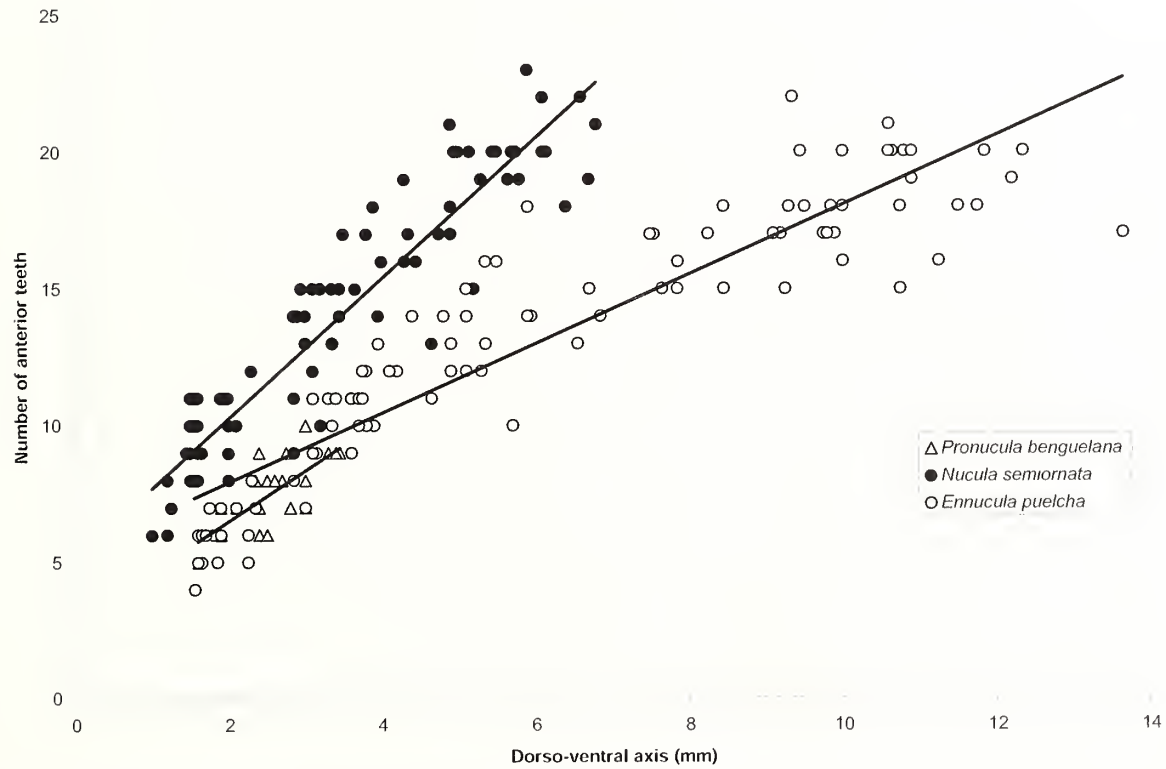


Figure 3. Relationship between: **A.** antero-posterior and **B.** dorso-ventral axes with the number of anterior teeth, showing the morphospaces overlap between *Pronucula benguelana* and *Ennucula puelcha*.

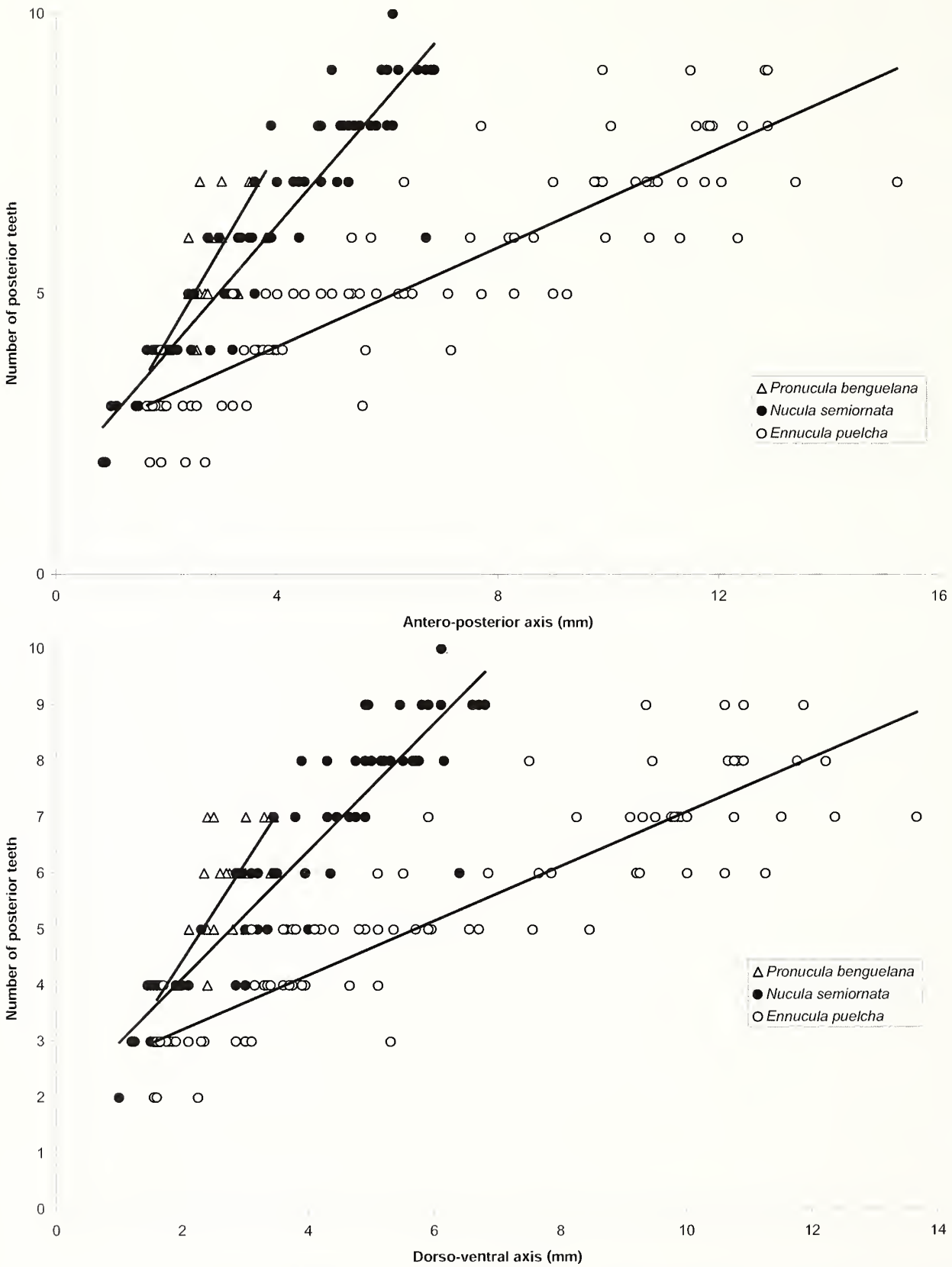


Figure 4. Relationship between: **A.** antero-posterior and **B.** dorso-ventral axes with the number of posterior teeth, showing the overlap of the morphospaces of *Pronucula benguelana* and *Nucula semiornata*.

RESULTS AND DISCUSSION

All the species studied exhibited a gradual increase of the number of anterior and posterior teeth during ontogeny. All results were statistically significant (Table 2), when we compared the importance of shell size with the number of anterior and posterior teeth. This statistical analysis confirmed the existence of a relationship between the two variables, size and number of teeth, and suggests that this relationship may be verified in other protobranch species. Furthermore, it confirmed the variation in the number of teeth for the same size class for each species studied. This attests to the inconsistency of this character when it is analyzed alone.

In addition, Figure 2 indicates a distinction among the genera *Adrana* and *Pronucula*, *Nucula*, and *Ennucula*, which becomes more evident when we compared the number of posterior teeth and the length of the dorso-ventral axis. This result matches most accepted classifications that consider several characters (not only number of teeth) and allocate these three genera into two distinct groups (e.g. Allen and Hannah, 1986; Maxwell, 1988; Giribet and Wheeler, 2002; Giribet, 2008).

On the other hand, considering the Nuculidae, the morphospace of *Pronucula bennetclana* overlapped with *E. puelcha* in the number of anterior teeth regressed on antero-posterior axis (Figure 3a) and on dorso-ventral axis (Fig. 3b); and *P. bennetclana* overlapped with *N. semiornata* in the number of posterior teeth regressed on antero-posterior axis (Figure 4a) and on dorso-ventral axis (Figure 4b). In both cases, these overlaps of the number of teeth (anterior or posterior) occurred up to about 4 mm in size, on each axis analyzed, for *P. bennetclana*. Because this latter species is about 4 mm in size, this size limit in the overlap cannot be interpreted as a consequence of the number of specimens collected.

It is evident that the current taxonomy of Nuculidae presents confused generic definitions, not rare with a great correspondence of characters. Considering only the results presented herein, the overlaps of the morphospaces of *Pronucula* and *Nucula* are in agreement, and may reinforce the view of Bergmans (1978), who synonymized the two genera, or that of Allen and Hannah (1986), who proposed the allocation of *Pronucula*, at a subgeneric rank, to the genus *Nucula*. Along the same lines, the overlaps of the morphospaces of *Ennucula* and *Nucula* may reinforce the view of Schenck (1934) who placed *Ennucula* as a subgenus of *Nucula*. Nevertheless, because no other taxonomic features were analyzed in this study and, moreover, none of the species studied are type-species of *Pronucula*, *Nucula*, or *Ennucula*, this ratification of the opinions of above-mentioned authors may be premature.

CONCLUSION

These statistical analyses confirmed empirical observations of the relation between shell size and number of teeth in protobranch bivalves and attests to the inconsistency of the latter character when analyzed alone. For the taxa studied herein, the number of teeth on the hinge is an important taxonomic feature, but only when the size of the shell is also taken into account. Otherwise, taxonomic studies and descriptions based only on the number of teeth without providing any measures of the shell are not informative and might make it impossible to define whether one is dealing with several similar species or just one that shows intraspecific variation for the character number of hinge teeth.

The use of other characters in the taxonomy of the group is obviously important, but for the species studied here, at the family level, the distinction between *Adrana* (Nuculanidae) and *Pronucula*, *Nucula*, and *Ennucula* (Nuculidae) is in agreement with most accepted classifications. This attests the importance of number of teeth on the hinge related to the size of the shell for the distinction of these two families even when no other characters are considered. Nevertheless, for the nuculids, the differentiation of the distinct genera is unclear. The number of teeth on hinge and the size of the shell alone do not provided a good distinction among the three genera and the overlap of the morphospaces of these different taxa reinforces the demand for the use of more taxonomic characters and emphasizes the need for more comprehensive studies with these groups.

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A new species of *Zeadmete* (Gastropoda: Cancellariidae) from South Carolina, a genus previously unknown in the Atlantic Ocean

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ABSTRACT

A new species of *Zeadmete* is described from deep water on the Blake Plateau southeast of Charleston, South Carolina. Previously known from South Africa, New Zealand, New Caledonia, and Fiji, this is the first report of *Zeadmete* from the Atlantic Ocean.

Additional keywords: Bathyal, deep-sea, gastropod

INTRODUCTION

The little-known genus *Zeadmete* has been recently discussed by Petit and Harasewych (2000) and Bouchet and Petit (2008). Previously known species occur off South Africa, New Zealand, New Caledonia, and Fiji. With the exception of *Zeadmete subantarctica* Powell, 1933, found at 65 m, this genus is usually found at 300–600 m depth. The new species extends this range to 764 meters.

Although known from only one specimen, the rarity of all known species, coupled with their depth, makes it advisable to describe the species. During extensive dredging on Norfolk Ridge (south of New Caledonia) only one specimen of *Zeadmete bilix* Bouchet and Petit, 2008, was discovered although it is several times larger than, and found in half the depth of, the new South Carolina species.

MATERIALS AND METHODS

In 1986, Lyle and Sarah Campbell were guest scientists with separate survey cruises on the SC Marine Resources Lady Lisa to determine if *Geryon* crabs were present in sufficient quantity to support a fishery off Charleston, South Carolina. *Geryon* are found in 600 to 1200 m of water, some 160 to 320 km offshore on the Blake Plateau. The Campbells were permitted to add a 30 cm diameter pipe dredge to the ballast holding down the crab traps, and a series of bulk sediment samples were obtained. Those constituted the first set of bathyal bulk sediment samples obtained from South Carolina waters. Mollusks were recorded by Dall (1889, 1927) from two similar samples off Florida and southern Georgia but there is virtually no published documentation of this fauna from South Carolina waters.

A sediment sample from SC Marine Resources Geryon cruise, 23 July 1986, Blake Plateau, southeast of Charleston, South Carolina from 418 fathoms (764 meters) water depth was recently washed for a student research project. Bulk sediment was wet screened through seven sieves ranging from 12.5 mm to 0.7 mm mesh. Preliminary investigation yielded 15 species of pelagic gastropods, 30 species of benthic mollusks, and other taxa ranging from fish otoliths to diverse benthic and planktic foraminifera. Ongoing investigations of remaining samples will more completely document the fauna.

One other species of Cancellariidae was found in the same sample as the new *Zeadmete*, a broken specimen of *Microcancilla microscopica* (Dall, 1889).

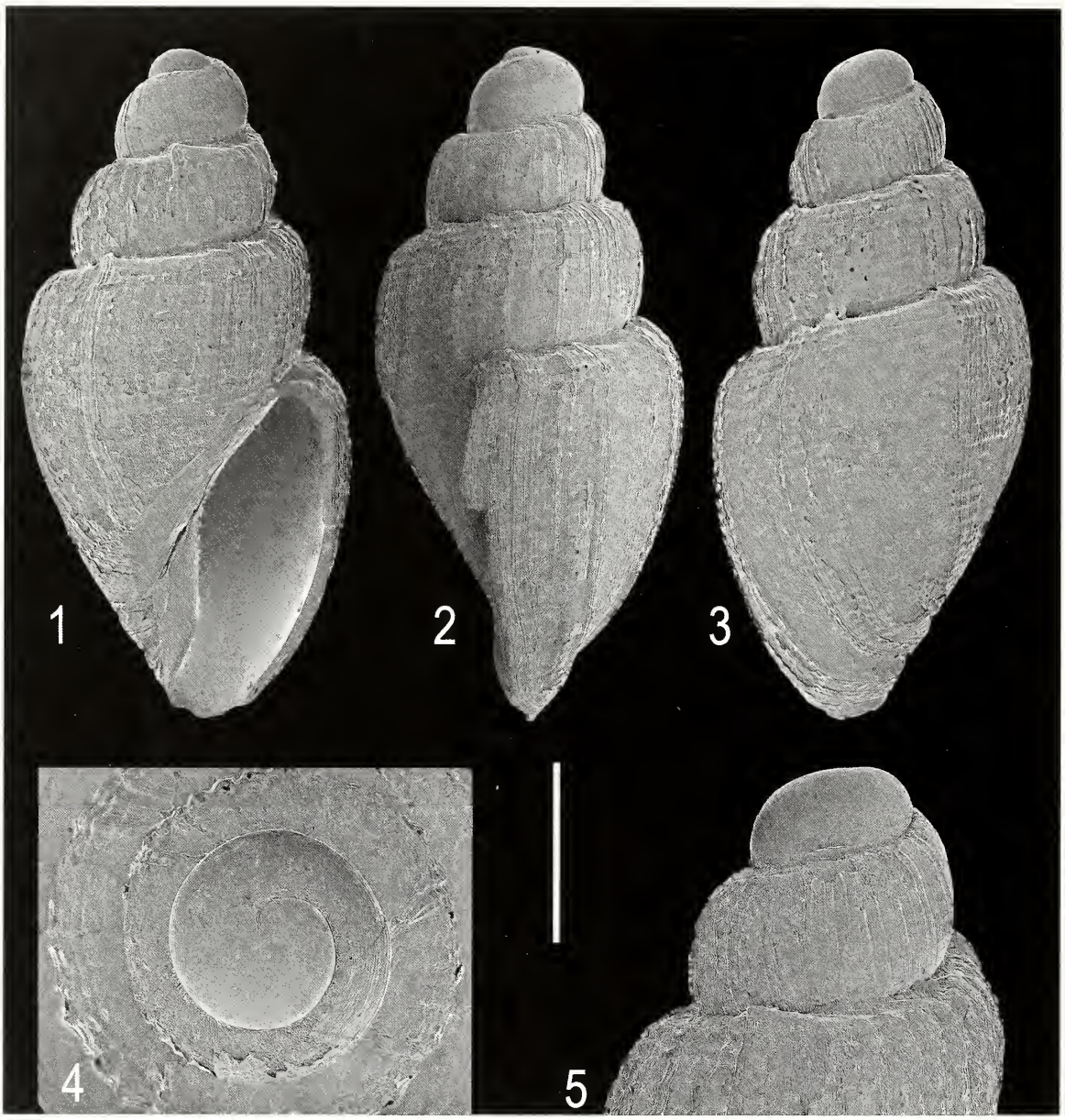
SYSTEMATICS

Family Cancellariidae Forbes and Hanley, 1851
Genus *Zeadmete* Finlay, 1926

Type Species: *Cancellaria trailli* Hutton, 1873, by original designation. Recent, New Zealand.

Zeadmete atlantica new species
(Figures 1–5)

Description: Shell (Figures 1–3) small (3.76 mm), elongated biconical, consisting of 3.75 whorls. Protoconch (Figures 4–5) smooth, evenly rounded, increasing in



Figures 1–5. *Zeadmete atlantica*. Southeast of Charleston, South Carolina, in 418 fathoms [764 m]. **1.** Apertural. **2.** Right lateral. **3.** Dorsal views of the holotype. **4.** Axial, and **5.** dorsal views of protoconch. Scale bar = 1 mm for entire shell, 500 µm for protoconch views.

diameter from 230 µm to 640 µm in 1 whorl, with fine, irregular spiral threads evident on last 0.5 whorl. Transition to teleoconch marked by onset of axial growth striae and fine ribs. Teleoconch of 2.75 roundly shouldered, weakly convex whorls. Suture deeply impressed. Axial sculpture of about 40 ribs per whorl, ribs becoming less distinct with increasing whorl size. Spiral sculpture of weak, narrow, evenly spaced spiral cords, about 30 on body whorl, 15 on penultimate whorl. Aperture 0.5 shell length, narrowly elliptical (W/L = 0.37), deflected from coiling axis by 16°. Outer lip strongly curved at shoulder, evenly convex from shoulder to tip of siphonal canal. Spiral sculpture most pronounced near shoulder and along siphonal canal. Inner lip with smooth inductural region that is slightly shorter than the smooth, axial columella, which lacks columellar folds, but has a single siphonal fold. Shell and aperture uniformly white in color.

Type Material: Holotype USNM 1125242 (3.76× 1.96 mm).

Type Locality: Blake Plateau, southeast of Charleston, South Carolina, 32°38.6′ N, 76°47.7′ W, 764 m (Geryon cruise, station 125, July 23, 1986).

Etymology: Named for the Atlantic Ocean.

Remarks: *Zeadmete atlantica* new species has a more rounded shoulder than most species in the genus. Although corroded, the type specimen differs from its geographically closest congener, the South African *Z. verheckeni* Petit and Harasewych, 2000, in having a rounded shoulder, more numerous axial ribs and less prominent nodules at the intersection of axial ribs and spiral cords. *Zeadmete bathymon* Bouchet and Petit, 2008, from New Caledonia has sculpture similar to *Z. atlantica* but the ribs are not as numerous and the shoulder is strongly angled.

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Current distribution of the exotic freshwater snail *Helisoma duryi* (Gastropoda: Planorbidae) in Brazil

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ABSTRACT

This article describes the current distribution of the introduced gastropod *Helisoma duryi* in Brazil. The species was recorded for the first time in Brazil in 1972, in Formosa, state of Goiás, and since then it has been reported to occur in the states of Ceará, Minas Gerais, Paraíba, Rio de Janeiro, and São Paulo. Recently, this species was found in the state of Ceará, where it was introduced through ornamental fish and aquatic plant trade. The expansion of the species range in Brazil demonstrates the need for increased efforts to monitor and control the introduction of exotic species. Up to now, *H. duryi* had been found in 14 municipalities together with specimens of Ampullariidae, Ancylidae, Corbiculidae, Lymnaeidae, Planorbidae, Physidae, and Thiaridae. We believe that the current absence of *H. duryi* in the localities where it had been previously collected (1972 and 1998) could be associated with environmental changes in those regions and also because selfing in *H. duryi* is not as efficient as it is for other Planorbidae species. A map with the distribution of *H. duryi* is also provided.

Additional keywords: exotic freshwater mollusks, biological invasions, invasive species, planorbids

INTRODUCTION

Non-native species, those that have been introduced from another geographic region to an area outside its natural range, have been the focus of several investigations in the past years, mostly because they have been closely related to problems in human health, in the environment, and economy. The Convention on Biological Diversity (CBD), ratified in 188 countries, including Brazil, is one of the most important international tools conceived to provide environmental conventions, strategies, and agreements in order to promote sustainable development. In Brazil, where specialists and environmental public bodies recognize the problems involved with exotic species, CBD signed the Decree number 2.519, seeking to protect and manage biodiversity (Ministério do Meio Ambiente, 2009).

Difficulties in predicting the effects of alien species after introduction were discussed by Meyer et al. (2008), in an investigation on the exotic giant African snail, *Achatina fulica* Bowdich, 1822. According to Ricklefs (2005), every invasion process undergoes four phases: introduction or colonization; settlement, which requires adaptation to local conditions to survive local species interactions; geographical expansion; and eventual decay. The period during which every species remains at each of those phases depends on either intrinsic or extrinsic factors to it. (Incidentally, Brazil is currently experiencing the explosive phase of the invasion of *A. fulica*, and dense populations of that species are widespread in at least 24 out of 26 Brazilian states and the Federal District.)

In Brazil, biological invasions and the pathways of introduction and spread of exotic species are not yet well documented, but a number of instances of the spread of invasive mollusks have been documented in the last decade: Thiengo et al. (2007a) reported the rapid expansion and current distribution of *A. fulica* since its introduction in the state of Paraná, in 1988 while Santos et al. (2002) and Fischer and Colley (2005) reported the occurrence *of A. fulica* in preservation areas in the states of Rio de Janeiro (Ilha Grande, Angra dos Reis) and Paraná (Ilha Rasa, municipality of Guaraqueçaba), respectively, and Takeda et al. (2003) and Mansur et al. (2004) reported the occurrence of the invasive freshwater clams *Limnoperna fortunei* (Dunker, 1857) and *Corbicula* spp. in Southern Brazil. In addition to environmental and economical problems related to exotic snail species, some of those species have medical and veterinary importance as they may be associated with zoonotic and parasitic transmission of diseases (Caldeira et al., 2007; Thiengo et al., 2008).

The aquarium trade is a major source of exotic freshwater mollusks. In 1972, a population of *Helisoma duryi* (Wetherby, 1879), autoehthonous from the Everglades wetlands in Florida, was first reported in Distrito de Santa Rosa, municipality of Formosa, state of Goiás, Brazil, in natural breeding sites connected with the Cana Brava River (Paraense, 1975). According to Paraense (1976), these speeimens collected in the locality Lagoa da Pedra, in connection with the Cana Brava River, ineluded a large number of albinos obtained from sympatrie populations of Ampullariidae, Ancylidae, Physidae, and other Planorbidae. Similarly, Thiengo et al. (1998) also reported the presence of albino specimens in fish tanks in the municipality of Guapimirim, state of Rio de Janeiro, Brazil, in June 1997 and remarked the importanee of aquarium fish trade in the introduction and spread of exotie snails in new sites.

Recognizing the threat to global biodiversity that invasive species play Brazil is one of 188 countries that have ratified the CBD in an effort to help manage this disappearing resource. In 2006 snails were sent from Serra Verde do Saraiva by the Secretaria de Saúde of the state of Ceará (SESA-CE), to the Centro Nacional de Referencia em Malacologia Médica (LRNM) for identifieation. These snails were identified as *H. duryi*, and prompted surveys of the present distribution of this species in Brazil along with the occurrence of sympatric freshwater snail species were performed and presented.

MATERIALS AND METHODS

Information on the distribution of *Helisoma duryi* in Brazil since its first recorded introduction was obtained from the literature and from data on specimens collected by the authors. Field surveys were performed in three states, from which the occurrence of *H. duryi* was previously reported by the staff of LRNM: Goiás (municipalities of Formosa and Vila Boa), Rio de Janeiro (municipality of Guapimirim), and Ceará (municipalities of Aearape, Fortaleza, Guaiúba, and Redenção).

In the state of Goiás (Table 1), snail collections were performed between 2003 and 2005 in wetland areas along federal highway BR-020, and in Lagoa da Pedra, between the municipalities of Formosa and Vila Boa. In the state of Rio de Janeiro (municipality of Guapimirim) colleetions were made in 2000, 2003, and 2007 (Table 1) in exotic ornamental fish (*Betta splendens* (Regan, 1910)) breeding tanks. Four municipalities were investigated in the state of Ceará (Table 1): three in the region of Serra Verde do Saraiva (Acarape, Guaiúba and Redenção) and one in the Fortaleza municipality (a lake named Lagoa de Porangabussu).

Mollusks were collected from different habitats (streams, wells, marshy areas, fish tanks and lakes) using collecting sieves. With the aim of assessing abiotic factors in the habitats where *H. duryi* occurs, variables sueh as temperature (water and air), pH, and the concentration of dissolved oxygen in the water column were measured using a mercurium thermomether, a pHmeter (Instrutherm pH-1700), and an oxymeter (Lutron DO-5510). Samples were maintained under laboratory conditions at LRNM in aquaria containing dechlorinated tap water and a thin bottom layer of a 2:1 mixture of screened soil and ground oyster shells as a source of mineral nutrients.

For specific identification, the snails were anesthetized with 0.05% sodium pentobarbital (Hypnol®) for five hours; killed by immersion in 70°C water and then fixed in Railliet-Henry solution (Fernandez et al. 2008). Snail samples were deposited in the Malacological Collection of Instituto Oswaldo Cruz (CMIOC).

RESULTS

In the state of Goiás (Table 1), eight freshwater gastropod species were found: *Biomphalaria straminea* (Dunker, 1848), *Drepanotrema anatinum* (Orbigny, 1835), *Drepanotrema cimex* (Morieand, 1839), *Drepanotrema depressissimum* (Moricand, 1839), *Drepanotrema lucidum* (Pfeiffer, 1839), *Gundlachia radiata* (Guilding, 1828), *Melanoides tuberculatus* (Müller, 1774) and *Pomacea* sp.

In the state of Rio de Janeiro, in the municipality of Guapimirim (Table 1), no *H. duryi* specimens were found but the following species were collected: *Biomphalaria tenagophila* (d'Orbigny, 1835), *B. straminea*, *Hebetancylus moricandi* (d'Orbigny, 1837), *Lymnaea columella* Say, 1817, *M.tuberculatus*, *Physa marmorata* Guilding, 1828, *Pomacea diffusa* (Reeve, 1856), and *Pomacea* sp. (only juvenile specimens).

In the state of Ceará, specimens of *H. duryi* were found in the two habitats, a well and a fish tank (Table 1). In these the water temperatures were 27.3°C and 27.4°C, environment temperatures were 36.8°C and 33.7°C, pH was: 7.76 and 6.38, and dissolved oxygen measured 7.8 mg/L and 7.0 mg/L in the well and the fish pond, respectively. The other freshwater gastropods found in the state were *B.straminea*, *D. lucidum*, *G. radiata*, *H. duryi*, *M.tuberculatus*, *P. marmorata*, *Pomacea lineata* (Spix in Wagner, 1827), *P. diffusa*, and *Pomacea* sp. (only juvenile specimens).

DISCUSSION

According to Paraense (1976) and the data from CMIOC, in August 1972, in addition to *Helisoma duryi*, the following snail species were collected in lakes formed by the Cana Brava River (in the municipality of Formosa, Goiás): *B.straminea*, *Biomphalaria schrammi* (Crosse, 1864), *D. anatinum*, *D. lucidum*, *Plesiophysa ornata* (Haas, 1938), *L. columella*, and *P. marmorata*. In the present study, surveys were performed in seven ponds formed by Cana Brava River flooded areas, in the municipalities of Vila Boa and Formosa, but no speeimens of *H.duryi* were found.

In the 1990s, many ornamental freshwater fish breeding facilities in the state of Rio de Janeiro were loeated in

Table 1. Study localities and species found.

State	Date	Municipality	Geographical coordinates	Biotope	Freshwater gastropods (Snail samples and respective the CMIOC collection number)
Goiás	March 2003	Vila Boa	15°03′54.6″ S, 47°04′44.8″ W	lake	*D. lucidum* (5199), *D. cimex* (5201), and *D. depressissimum* (5200)
		Formosa	15°29′57.5″ S, 47°06′37.8″ W	lake	No freshwater snail was found.
	May 2005	Vila Boa	15°02′19.9″ S, 47°12′04.2″ W	lake	No freshwater snail was found.
		Vila Boa	15°02′39.1″ S, 47°12′22.5″ W	lake	*D. anatinum* (5191), and *M. tuberculatus* (5190)
		Vila Boa	15°04′10.8″ S, 47°04′20.9″ W	lake	*B. straminea* (5193), *D. anatinum* (5192), *D. lucidum*, *G. radiata* (5194), and *Pomacea* sp.
	August 2005	Vila Boa	15°04′09.3″ S, 47°05′24.1″ W	lake	*B. straminea* (5195), *D. anatinum* (5196), *D. cimex*, and *D. lucidum* (5198)
		Vila Boa	15°04′03.8″ S, 47°05′40.4″ W	lake	*B. straminea*, *D. anatinum*, *D. cimex*, *D. lucidum*, *G. radiata* (5197), and *M. tuberculatus*
Rio de Janeiro	January 2000	Guapimirim	22°38′21.7″ S, 42°58′54.0″ W	fish tank	No freshwater snail was found.
	September 2003	Guapimirim	22°38′21.7″ S, 42°58′54.0″ W	fish tank	*B. tenagophila*, *B. straminea*, *L. columella*, *M. tuberculatus* and *P. marmorata*
	January 2007	Guapimirim	22°38′21.7″ S, 42°58′54.0″ W	tanks	*B. tenagophila*, *H. moricandi*, *M. tuberculatus*, *P. marmorata*, *P. bridgesii* and *Pomacea* sp.
Ceará	October 2006	Acarape	04°11′03.9″ S, 38°43′24.9″ W	lake	*M. tuberculatus* (5147) and *Pomacea* sp. (5202)
		Acarape	04°11′45.3″ S, 38°42′55.7″ W	lake	*B. straminea* (5149), *D. lucidum* (5151), *G. radiata* (5150), *M. tuberculatus* (5148) and *P.lineata* (5203)
		Guaiúba	04°10′32.1″ S, 38°44′02.2″ W	three wells	*B. straminea* (5153), in one of them
	October 2006	Redenção	04°10′48.9″ S, 38°43′48.0″ W	well	No freshwater snail was found.
		Redenção	04°10′55.8″ S, 38°43′40.8″ W	well	No freshwater snail was found.
		Redenção	04°10′41.2″ S, 38°43′51.4″ W	well	*H. duryi* (5152)
		Redenção	04°10′25.3″ S, 38°43′52.7″ W	well	No freshwater snail was found.
		Redenção	04°10′50.6″ S, 38°43′45.3″ W	stream	No freshwater snail was found.
		Redenção	04°10′27.2″ S, 38°43′49.8″ W	lake	*G. radiata* (5154) and *P. lineata*
		Redenção	04°10′46.8″ S, 38°44′02.4″ W	fish tank	*H. duryi* (5157), *P. marmorata* (5156) and *P. diffusa* (5204)
		Fortaleza	03°44′45.4″ S, 38°32′00.0″ W	lake	*P. lineata* (5146) and *B.straminea:* only shells
	August 2008	Fortaleza	03°44′37.4″ S, 38°32′57.8″ W	lake	*P. lineata* and *B.straminea*

the municipality of Guapimirim. This probably favored the introduction of exotic species. According to the field work registrations in the LRNM, specimens of *H. duryi* reported by Thiengo et al. (1998) were found in sympatry with *B. straminea*, *Ferrissia* sp., *L. columella* and *P. bridgesii*. The latter is identified as *P. diffusa* nowadays, according to Hayes et al (2008). Many albino specimens of *H. duryi* and *P. diffusa* were also found in those fish tanks in September, 1997. Although no *H. duryi* specimen was found, the present paper confirms the establishment of *P. diffusa*, only species reported by Thiengo et al. (1998) and also obtained in 2007. This species occurs naturally throughout the Amazon Basin (Peru, Bolivia and Brazil) but it is widespread nowadays due to aquarium and fish trade, specially the more attractive albino specimens known as golden apple snails.

Our results indicate a reduction in *Helisoma duryi* populations in the state of Ceará. In March and May 2006, a team from Secretaria de Saúde of the state of Ceará (SESA-CE) collected samples of *H. duryi* in five localities in the municipalities of Redenção and Guaiúba, and in the present study this species was found in only two of these (Table 1). In the lake Porangabussu, in the

municipality of Fortaleza, where *H. duryi* and *M. tuberculatus* specimens were collected in 1999 by Dr. Fernando Bezerra (Universidade Federal do Ceará) and sent to LRNM for identification, no specimens were found in 2006 and 2008.

The introduction of *Helisoma duryi* was probably the result of aquaculture activity. Ornamental plants are used in fish tanks chiefly to promote water oxygenation. These plants may transport both eggs and early stages of freshwater gastropods, enabling their spread into new environments. Correa et al. (1980) inferred the importance of such plants as vectors for dispersal of non-native mollusks, and noted that they may have been particularly important regarding the spread of schistosomiasis-carrying individuals of *B. straminea* in São Paulo state. They surveyed aquarium and aquatic plant shops throughout the municipality and found specimens of Physidae, Lymnaeidae, Ampullariidae, Thiaridae, and Planorbidae, including *Helisoma* sp. In the same state, França et al. (2007) collected sediment samples in three reservoirs of the Baixo Rio Tietê (Promissão, Nova Avanhandava, and Três Irmãos), in November 2002 and August 2003, in order to identify species of benthic mollusks. Specimens *H. duryi* were found, including another exotic bivalve, *Corbicula fluminea* (Muller, 1774), and the Afro-asiatic gastropod, *M. tuberculatus*. Although *H. duryi* was present in the three reservoirs analyzed, that species had the lowest density among the exotic mollusks.

For an exotic species to be regarded as invasive it must have, at least, considerable adaptability to new environments, rapid sexual maturation, and a large reproductive capacity (Santos et al. 2007). Ecological and parasitological laboratory studies of *Helisoma duryi* obtained in Goiás in 1972 (Milward-de-Andrade, 1978a, b; Milward-de-Andrade and Belisário, 1979; Milward-de-Andrade and Souza, 1979; Milward-de-Andrade et al., 1979) indicate adaptive advantages of that exotic species over *Biomphalaria glabrata* (Say, 1818). These include a higher reproduction rate, lower mortality, higher resistance to environmental desiccation, increased starvation survival, and increased resistance to infection by *Schistosoma mansoni* in that former species.

Other authors reported that *Helisoma duryi* may have the ability to control populations of *Biomphalaria* spp., a vector of schistosomiasis (Frandsen, 1987; Frandsen and Madsen, 1979), in Puerto Rico, St. Lucia, Egypt, and Tanzania. In Brazil, Milward-de-Andrade (1979) argued that the capacity of *H.duryi* to colonize Neotropical ecosystems, either directly or indirectly, may play a key role in the biological control of schistosomiasis mansoni. However, throughout the last three decades, such expected interspecific competition has not been observed (the *H. duryi* population found in 1972, in Goiás, did not succeessfully establish itself, and was not observed in 2003 and 2005). Remarkably, *M. tuberculatus* was found in this habitat after 2005, having been introdueed in Brazil probably by aquarists in Santos in 1967 (Vaz et al., 1986). Currently, *M. tuberculatus* may be found in seventeen Brazilian states and in the Distrito Federal, in both lenthic and lothic habitats, with or without anthropic influences (Fernandez et al., 2003).

Melanoides tuberculatus reproduces parthenogenetically, which may account for its wider geographic distribution when compared to *H. duryi*. The latter may occasionally utilize selfing as an alternative means of reproduction, although it is not as efficient as it is for other Planorbidae species (Paraense and Corrêa, 1988). According to these authors, *H. duryi* benefits much less from functional hermaphroditism which, besides other advantages, enables a single virgin individual to found a new population. Furthermore, other characteristics of *M. tuberculatus*, such as viviparity, iteroparity and high survival rate of the young, may also contribute to its spread (Santos et al., 2007).

In Guapimirim (Rio de Janeiro) and in Lagoa do Porangabussu (Ceará), *B. straminea* appears to have adapted to local conditions, forming colonies, while *H. duryi* has not. Remarkably, in Guapimirim municipality, specimens of *B. straminea* were found in 1997 and 2003, but not in 2007; whereas *B. tenagophila* was recorded in 2003 and 2007. The disappearance of *B. straminea* and the establishment of *B. tenagophila* must be confirmed. In contrast, Silva et al. (1997) reported the replacement of *B.straminea* for *B.tenagophila* in the municipality of Paraeambi, Rio de Janeiro.

The introduction of *H. duryi* in the state of Ceará may be a result of *B. splendens* aquaculture (breeding and trade), similar to that described for Guapimirim (Rio de

Figure 1. *Helisoma duryi* from Ceará state, municipality of Redenção (04°10′46.8" S, 38°44′02.4" W).

Janeiro). Ornamental and pet fish such as *B. splendens* originate in Asia and were introduced to Europe and the United States in 1874 and 1910, respectively (Faria et al., 2006). In the 1960s and 1970s, ornamental fish breeders in Brazil introduced production techniques and female individuals imported from Europe and the United States. Since then, individuals of *H. duryi* have been recorded in the following Brazilian states: Minas Gerais, in the municipalities of Viçosa in 1967, and Uberaba (Vidigal et al., 2000); Rio de Janeiro, in the municipality of Nova Iguaçu in 1975; Paraíba, in the municipalities of João Pessoa and Campina Grande (Abilio, 2003); and São Paulo (Corrêa et al., 1980; França et al., 2007). The distribution of the exotic freshwater snail *H. duryi* in Brazil is shown in the Figure 1.

In addition to use of the species in ornamental fish aquaculture, *Betta splendens* was also released under experimental conditions in 2000 as a biological control of the mosquito *Aedes aegypti* Linnaeus, 1758, in the state of Ceará, municipalities of Fortaleza and Canindé (Pamplona et al., 2004). This may in part account for the spread of *H. duryi* in that state. A temporary shortage of rainfall in the state of Ceará in October 2006 made it difficult to find *H. duryi*, in contrast to March and May, the rainfall season in that region. In October 2006, *H. duryi* specimens (juvenile and eggs) were found in a fish tank of ornamental fish production in Redenção, as well as other snail species such as *P. marmorata* and *P. diffusa*. Recently, Hayes et al. (2008) reported that some ampullariid species, such as *P. diffusa*, may have some characteristics that allow them to become invaders following introduction; its occurrence in Guapimirim (Rio de Janeiro), ten years after its first record, supports Hayes's remark. Furthermore, the presence of *P. diffusa* in Ceará, currently restricted to a fish tank, is reason for concern over the potential for future spread and establishment of new colonies in other areas of Serra Verde do Saraiva. This could happen as a result of the rainy season, a possibility that in itself makes evident the urgent need for monitoring of the local malacofauna.

To date, there is no record of threatened native species, risk of economical loss, or damage to public health that could be triggered by the introduction of *Heliosma duryi* in Brazil. However, this lack of concern may be unwarranted, and preventive measures against the introduction and spread of the species, as well as of others that

Figure 2. Distribution of the exotic freshwater snail *Helisoma duryi* in Brazil: 1, Fortaleza; 2, Guaiúba; 3, Aearape; 4, Redenção; 5, Campina Grande; 6, João Pessoa; 7, Vila Boa; 8, Formosa; 9, Uberaba; 10, Viçosa; 11, Promissão; 12, São Paulo; 13, Nova Iguaçu; 14, Guapimirim.

are associated with environmental damages and public health problems, should be taken. Accordingly, strict law enforcement policies and procedures must be established in the trade of aquatic plants to fish producers as a preventive measure to preserve our biodiversity.

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Early stages of development in the endangered limpet *Patella ferruginea* Gmelin, 1791 (Gastropoda: Patellidae)

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ABSTRACT

The larval biology of *Patella ferruginea* is studied for the first time. Development in the species first showed two complete and equal cleavages whereas the third cleavage was unequal, resulting in an embryo with 4 micromeres and 4 macromeres. Early trochophores were detected 19 hours post-fertilization and pretorsional veligers appeared 27 hours post-fertilization. Early stages of development are very similar to those shown by other related limpet speeies, with higher developmental times than those recorded for *Patella caerulea* and similar to those obtained in *Patella vulgata*. However, *in vitro* fertilization and the obtainment of spats in a massive amount could be the solution for replenishing threatened or extinct populations of this extremely endangered Mediterranean speeies. The results of the present study represent a first approach in order to produce great amounts of spats in laboratory conditions for further reintroduction projects aiming for conservation of the species.

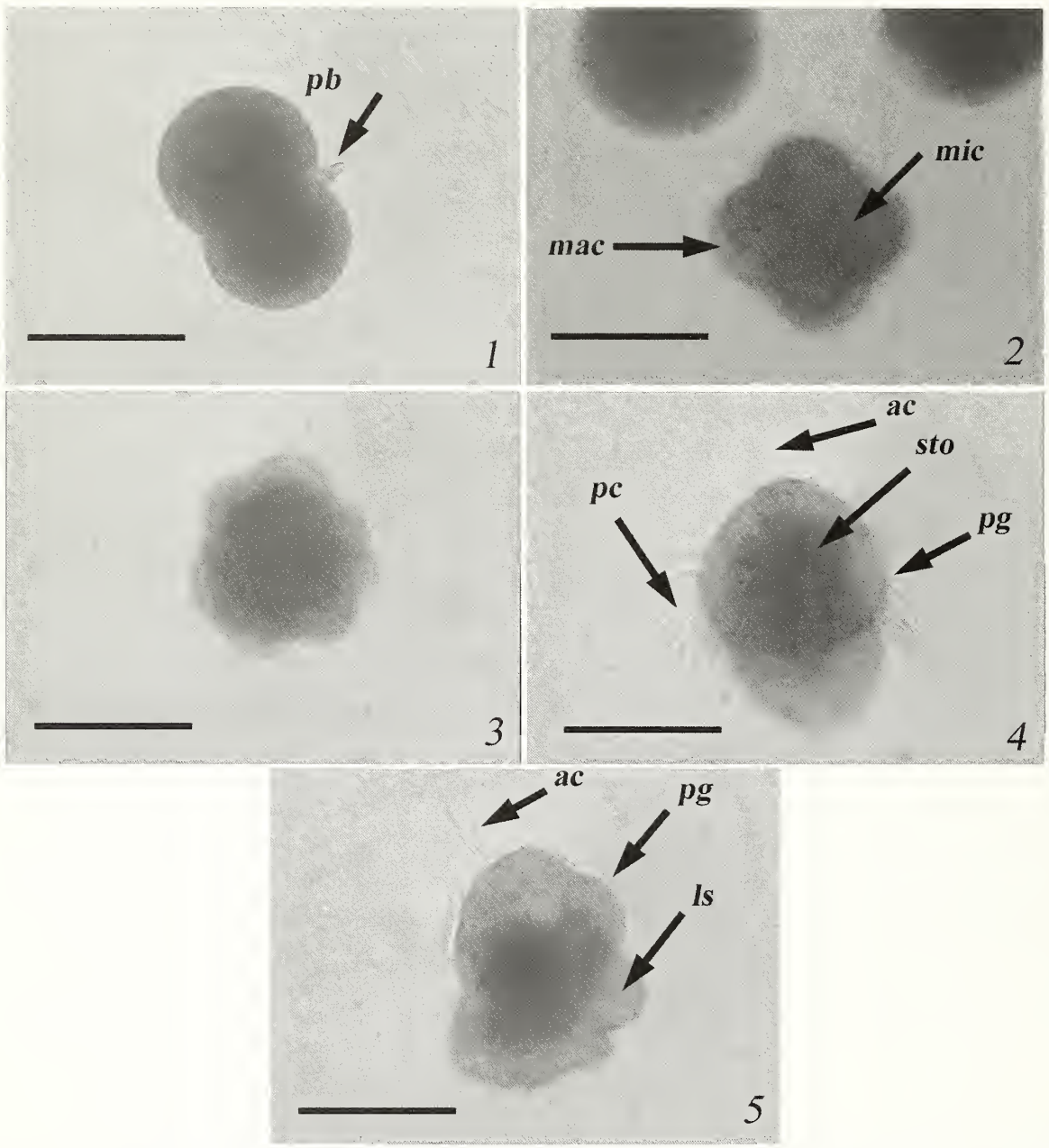
Additional keywords: Conservation, endangered speeies

INTRODUCTION

The mollusk *Patella ferruginea* Gmelin, 1791, endemie to the Mediterranean, is the most endangered marine species listed on the European Council Directive 92/43/EEC and it is presently under serious risk of extinction (Laborel-Deguen and Laborel, 1991; Ramos, 1998; Espinosa et al., 2006). Nevertheless, its biology and ecology are poorly known (Guerra-García et al., 2004) and studies mainly foeused on the reproductive biology and larval development of the species are urgently required, as pointed out by Templado (2001) and Guallart et al., (2006), in order to implement adequate management and eonservation strategies. The larval biology has not been studied in detail before, although some preliminary fertilization assays were made on the field by Guallart et al., (2006). Taking into account that in the last decades captive breeding has been suggested an important supportive intervention to avoid the loss of many speeies (IUCN, 1987), *in vitro* fertilization of *Patella ferruginea* and the obtainment of spats in a massive amount could be the solution for replenishing the threatened or extinct populations of the species around the Mediterranean. The development of appropriate culture techniques is considered to be crucial for the future conservation of the species.

MATERIALS AND METHODS

Adults of *Patella ferruginea* were collected from Ceuta, North Africa (35°53′20″ N, 5°18′30″ W), during October and November 2006, overlapping with the annual reproduction period of the species (Frenkiel, 1975) and independently of the lunar cycle, but always during low tide. Animals were kept in an aquarium, at a constant temperature of 18°C. Additionally, and in order to determine the maturation stage of the gonads, biopsies were taken. The gonads of ripe animals were dissected for artificial insemination following Van den Biggelaar (1977) and Wanninger et al. (1999) protocols; all further fertilization, culture, and breeding procedures were earried out in Seachem® artificial seawater filtered through a 0.45 µm mesh (AFSW) at 18°C. 1000 ml beakers were used as culture vessels, each filled with 500 ml of AFSW, stirred through moderate aeration. Eggs from four females were treated with alkaline sea water (pH = 8.9, by addition of drops of NH_4OH) for 1–7 minutes before fertilization to induee the egg-ripening proeess, followed by stirring, allowed to settle for 3 minutes, washing, and decanting 4 or 5 times (see also Dodd, 1957). Sperm of four males was diluted in AFSW until the suspension beeame fully clear; the agility of sperm cells was confirmed under the microscope before insemination. For fertilization, 10–20 drops of sperm suspension were used per liter of egg-eontaining AFSW. The percentage of fertilized eggs at each treatment was assessed using a compound microscope by the presenee of normal or abnormal cleavage in 100 undamaged eggs that were



Figures 1–5. Development stages in *Patella ferruginea*, reared at 18°C. Light micrographs. **1.** First cleavage (2 h) displaying polar body (**pb**). **2.** Eight-cell stage (4 h). Micromeres (**mic**); macromeres (**mac**). **3.** >12 cells: morula (5 h). **4.** Completely formed trochophore (19 h) with apical cilia (**ac**), prototrochal cilia (**pc**), prototrochal girdle (**pg**) and stomodeum (**sto**). **5.** Early pretorsional veliger (27 h) with apical cilia (**ac**), prototrochal girdle (**pg**) and larval shell (**ls**). Scale bars 100 µm.

randomly sampled from each vessel at least 4 h after insemination (see Baker and Tyler, 2001).

Larval cultures were kept in AFSW with 50 mg streptomycin and 60 mg penicillin per litre to minimize microbial or fungal infection. The water was changed periodically by pouring the vessels' content on to a sieve of 100 µm being held partly under water to prevent damage to the larvae. Larval development was monitored with a compound microscope, and major stages were recorded with photomicrographs.

RESULTS

Eggs of *Patella ferruginea* present an average diameter of 149.78 µm whereas sperm shows an average length of 3.78 µm (Espinosa et al., 2006). The first evidence of fertilization was the extrusion of the first polar body in the first two hours after insemination, and the completeness of the first two cleavages, equal and always initiated near the polar body (Figure 1). However, the fertilization rate resulted very low (3±1%). The third cleavage was

unequal and equatorial, such that the resulting 8-celled embryos were composed of 4 macromeres and 4 micromeres (Figure 2). Trocophores presented the natural morphology associated with the taxon and swam actively during 19 hours after fertilization, with telotroch (anal tuft), apical and prototrochal cilia (Figure 4) well developed and similar to those described for other patellid limpet species. In early trochophores, steady swimming was often alternated with abrupt bursts of speed. This sprint behaviour was constantly observed. Trochophores swam horizontally and vertically in culture vessels. The stomodeum was visible immediately beneath the prototrochal girdle (Figure 4). In pretorsional veliger the larval shell started to be observed (Figure 5) 27 hours after fertilization, whereas other structures remained, as the apical cilia and prototrochal girdle. This pretorsional veliger could be observed until 48 hours after fertilization, when the remained larvae died.

DISCUSSION

The early stages of larval development in *Patella ferruginea* obtained in the present study, appear to be very similar to other related limpet species, with higher developmental times than *Patella caerulea* (see Wanninger et al., 1999) and similar to those obtained in *Patella vulgata* (see Dodd, 1957; Wanninger et al., 1999). Nevertheless, it is known that water temperature influences the timing of developmental events (Kay and Emlet, 2002). In this sense, the proportional timing for *P. ferruginea* could be higher than for *P. vulgata*, although further experiments would be necessary. It is important to note that the fertilization rates obtained were very low and that the larval survival did not exceed 48 h, despite the use of similar methods that have reported good results in other related species (Dodd, 1957; Wanninger et al., 1999, 2000; Kay and Emlet, 2002). Further studies are required in order to establish if these results can be imputed to the necessity of improving the methodology or to biological constraints of the species.

Either way, the results of the present study could be considered as a first step towards the elaboration of a protocol that will permit to rear spats in laboratory conditions which could be used for further reintroduction and conservational projects.

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A review of the Recent Pandoridae (Bivalvia) in the Panamic Province, with descriptions of three new species

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ABSTRACT

Six genera and 16 species of Panamic Pandoridae are described and illustrated. Three species are described as new, namely *Pandora* (*Pandora*) *rachaelae*, *Pandora* (*Pandorella*) *sarahae*, and *Clidiophora dorsorectus*, and one new genus, *Coania*. Diagnoses are provided for the genera, subgenera, and species, as well as illustrations of the type specimens of the nominate species. *Frenamya*, *Clidiophora*, *Heteroclidus*, and *Foveadens* are herein elevated to generic rank. The high diversity of Pandoridae in the tropical Panamic Province is compared with other tropical regions along with more temperate climes.

INTRODUCTION

The Greek myth of Pandora portrays her as the first mortal woman, one of exceptional beauty. Pandora also opened the forbidden box, releasing all the evils of humankind. So it is with the members of the bivalve family Pandoridae, species of amazing beauty, but also those with taxonomic confusion and peril. We herein review the Pandoridae of the Panamic Province, accompanied by full descriptions, diagnostic characters between genera and species, and provide photographs of types and typical specimens.

The functional morphology of the Atlantic *Pandora inaequivalvis* (Linnaeus, 1758) and *P. pinna* (Montagu, 1803) was detailed by Allen (1954). The biology and functional morphology of the Pacific *P. filosa* was examined by Thomas (1994). Through experimental studies, Allen and Allen (1955) postulated that the primary life position of *P. inaequivalvis* is with the curved side down, but the species is capable of surviving in almost any orientation for considerable periods. However, Allen and Allen also noted that specimens buried more than 2 cm below the sediment surface had a low rate of survival, which likely limits the distribution of most *Pandora* to low energy habitats. Additional pandorid functional morphology was elucidated by Yonge and Morton (1980) and Morton (1984), with particular emphasis on the ligament and lithodesma. The functional morphology and natural history of all Panamic Pandoridae remains undocumented.

In their monograph of the Western Atlantic Pandoridae, Boss and Merrill (1965) presented the first modern review of the family in the New World. Due to a paucity of literature at the time, they postulated that the family is not diverse in the tropical regions, a hypothesis which will be refuted by the data herein. Importantly, Boss and Merrill provided detailed anatomical descriptions and precise illustrations to accompany their shell morphology descriptions. Unfortunately, subsequent workers did not follow the dentition and ligament nomenclature defined in this important paper.

Boss (1965) included all known generic, subgeneric, specific, and subspecific names in the Pandoridae. This has provided a base for our current research, in particular with documenting generic and subgeneric names.

Panamic pandorids were first described by G.B. Sowerby, I (1835), in his review of new species collected by Cuming in South America. Carpenter (1856, 1865) described additional species from Mexico, and Dall (1915) added more species from Mexico and Panama. Keen (1958) presented the first complete accounting of the Panamic pandorids, including diagnoses of *Pandora* subgenera and illustrations of several type specimens, and slightly revised this treatment thirteen years later (Keen, 1971). Olsson (1961) provided keys to the southern Panamic *Pandora* subgenera and species, and extended the geographic distribution of several species.

Thus, with the seemingly ardent work by the authors above, we were perplexed to have great difficulty identifying common pandorid species in the Panamic Province. When examining museum and private collections we found that the identifications were almost random, with little continuity between identifications, sometimes even within a single collection. Upon examination of the type specimens of the Panamic species, we further noted that most of the species in collections were incorrectly identified. It was with this backdrop that we

developed the diagnoses below, with a goal of providing useful tools to identify this difficult and plastic group of bivalves.

Abbreviations and Text Conventions: Each valid taxon is followed by a synonymy, a description, distribution and habitat data, information on type specimens and type locality, and additional remarks about the taxon. Distribution information is based on Recent specimens we have examined, unless otherwise noted. We have not examined any fossil material. Sadly, no wet preserved specimens were located during this study, thus we did not describe the anatomy of the species covered below. All references to valve convexity and concavity refer to the external view the specimens.

Abbreviations used in the text are as follows: BMNH – The Natural History Museum, London, United Kingdom; CAS – California Academy of Sciences, San Francisco, California, USA; LACM – Natural History Museum of Los Angeles County, Los Angeles, California, USA; MCZ – Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA; PRI – Paleontological Research Institution, Ithaca, New York, USA: SBMNH – Santa Barbara Museum of Natural History, Santa Barbara, California, USA; UMML – University of Miami Marine Laboratory, Rosenstiel School of Marine and Atmospheric Science, Miami, Florida, USA; USNM – National Museum of Natural History, Smithsonian Institution, Washington DC, USA.

SYSTEMATICS

Pandoridae Rafinesque, 1815

Diagnostic characters between genera and subgenera are given in Table 1, and species-level characters are given in Table 2.

Genus *Pandora* Bruguière, 1797

Pandora Bruguière, 1797. Type species (SD Children, 1823): *Pandora rostrata* Lamarck, 1818, = *Solen inaequivalvis* Linnaeus, 1758. Recent, Mediterranean.

Description: Shell strongly inequilateral, posterior end longer; right valve flat to concave; left valve flat to convex; hinge plate vestigial to well developed, with weak to strong cardinal teeth bordering resilifer; lithodesma usually present; sculpture of irregular commarginal striae or ribs, some with radial ribs or grooves; interior nacreous. Siphons short.

Distribution: The genus is cosmopolitan in distribution, found from intertidal to abyssal depths.

Remarks: Considered by Boss and Merrill (1965) to be primarily a cold-water genus, the findings in this paper indicate a high tropical diversity. It is likely other tropical regions have a much higher diversity than currently reported.

Subgenus *Pandora* sensu stricto

Hinge of left valve narrow, greatly reduced, anterior cardinal tooth a small tubercle or broadly flattened, posterior cardinal tooth absent to reduced. Right valve with small to moderate anterior cardinal tooth, posterior tooth short to moderately long. Exterior sculpture of commarginal striae or ribs, some with very faint radial striae.

Pandora (*Pandora*) *brevifrons* G.B. Sowerby I, 1835 (Figure 1)

Pandora brevifrons G.B. Sowerby I, 1835: 93.

Description: Shell Shape: Ellipsoid-elongate; very inequivalve, left valve very inflated, right valve very concave; entire shell strongly twisted dorsoventrally; anterior end short; anterodorsal margin straight; posterior end attenuate, without discrete rostrum; ventral margin of left valve broadly rounded, slightly straighter mid-ventrally.

Sculpture and Color: Anterior end of left valve not set off by a change in sculpture or color; left valve with 2 low radial ribs extending from beaks to posterior margin, commarginal striae over entire valve; right valve sculpture of fine commarginal striae, with long, deep, furrow along posterodorsal margin.

Hinge: Left valve with anterior tubercle, and an elongate, oblique resilifer; right valve with two short, subequal cardinal teeth; lithodesma unknown.

Muscle Scars: adductor muscle scars subequal, subcircular.

Length: to 22 mm [BMNH].

Distribution: Currently only known from the type locality at Bahía Panamá, Panama (9.0°N) [BMNH].

Type Material: BMNH 1966572, 3 syntypes - paired valves.

Type Locality: Panama, 18 m (originally 10 fathoms), sandy bottom.

Remarks: Records from the region around San Felipe, Baja California, Mexico (Gemmell et al., 1987; Dushane and Brennan, 1969) are *Pandora sarahae* new species.

In spite of intensive collecting in Panamá, this species has not been found since its description in 1835. It is possible that the type is mislocalized. However, study of specimens from adjacent and far reaching provinces has also not yielded any material of this species.

Literature: Keen (1971: 287), Olsson (1961: 454).

Pandora (*Pandora*) *rachaelae* new species (Figures 2–4)

Description: Shell Shape: Ovate-elongate; inequivalve, left valve slightly inflated, right valve flat; posterodorsal margin of right valve overlapping left, ventral margin of left valve overlapping right; entire shell not twisted to slightly twisted; anterior end short; anterodorsal margin slightly recurved; posterior end broadly rounded, with wide, short, truncate rostrum; ventral margin broadly rounded, with

Table 1. Generic and subgeneric characteristics of the Pandoridae in the Panamic Province.

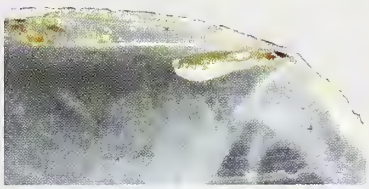
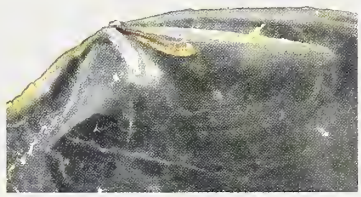
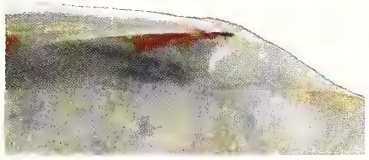
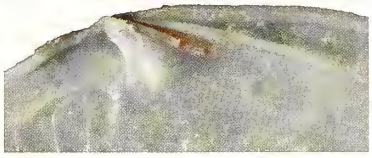
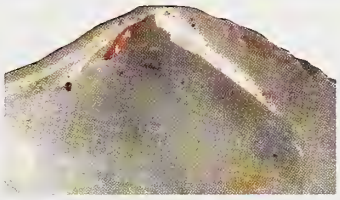
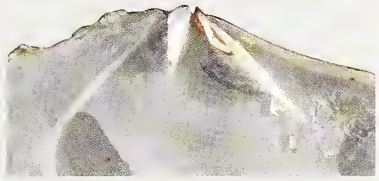
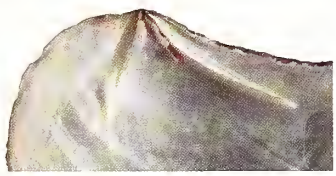
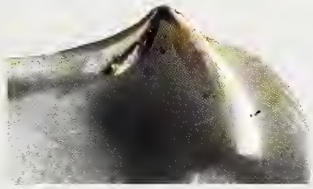
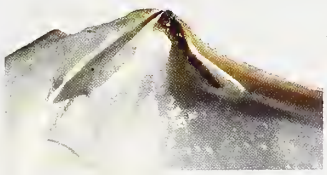
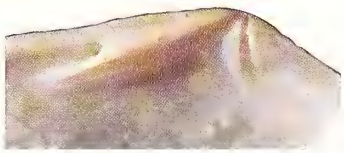
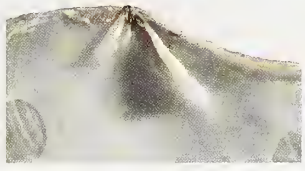
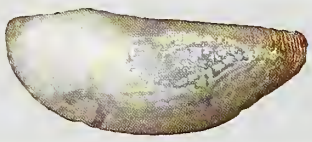
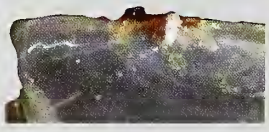
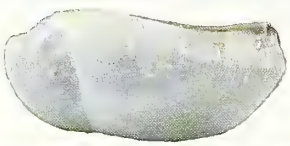
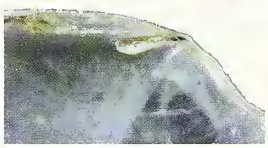
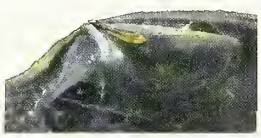
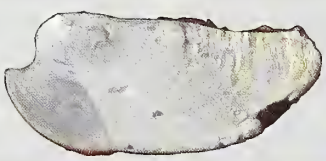
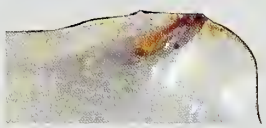
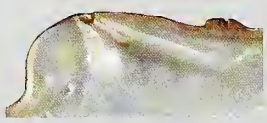
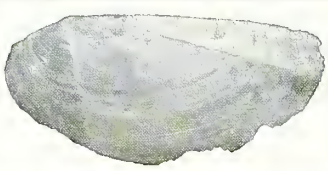
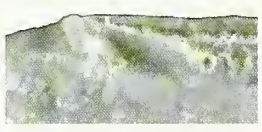
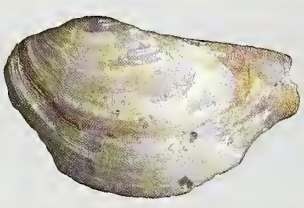
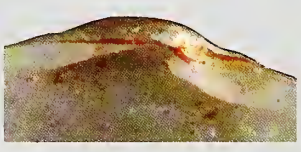
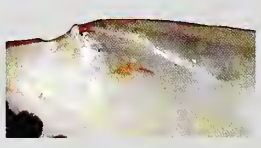
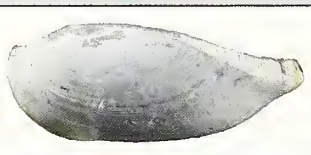
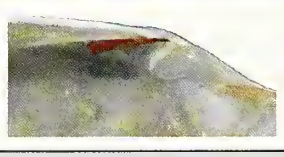
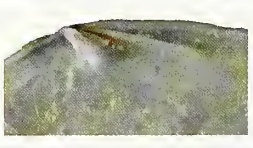
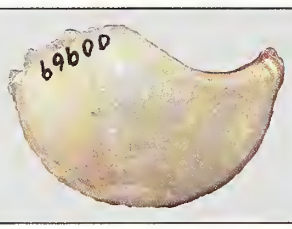
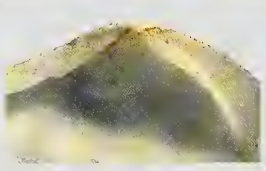
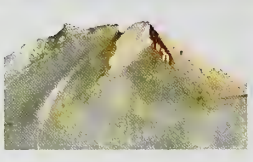
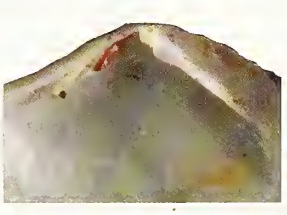
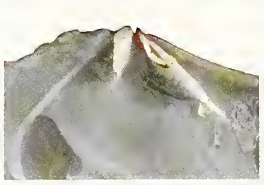
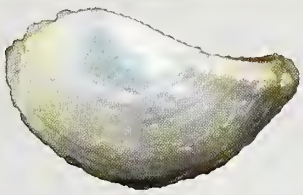
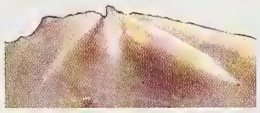
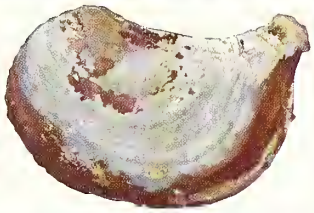
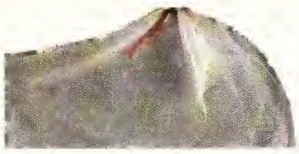
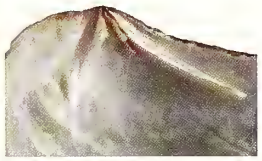
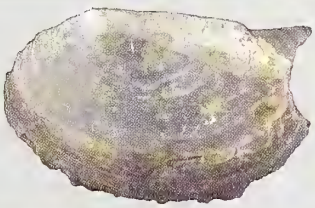
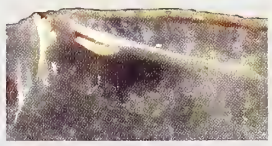
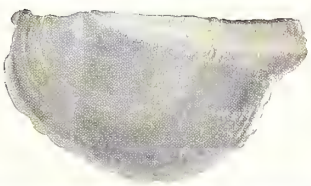
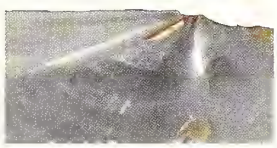
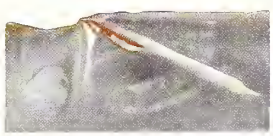
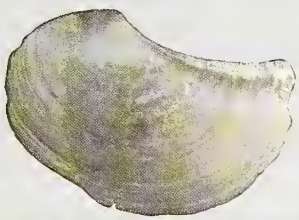
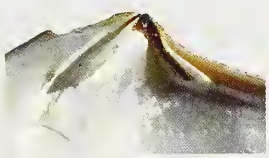
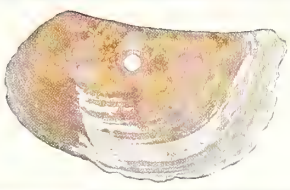
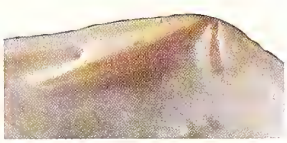
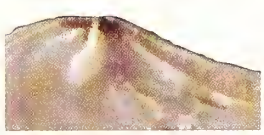
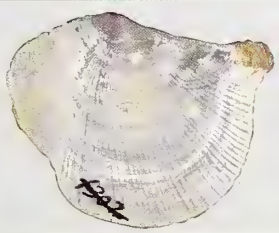
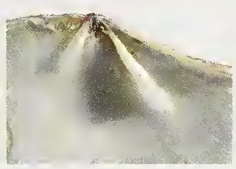
Genus (Subgenus)	Sculpture of valves	Left hinge	Right hinge
Pandora (*Pandora*)	right valve commarginal only		
Pandora (*Pandorella*)	right valve with radial grooves		
Frenamya	right valve commarginal only	 anterior tooth, ends anterior of adductor scar	
Clidiophora	right valve commarginal only	anterior tooth, ends posterior of adductor scar	
Heteroclidus	right valve commarginal only	 anterior tooth, ends anterior of adductor scar	
Foveadens	right valve commarginal only		
Coania	right valve with radial grooves; left valve with radial ribs		

Table 2. Species characteristics of the Pandoridae in the Panamic Province.

Taxa	Shell Shape	Left Valve Dentition	Right Valve Dentition
Pandora (Pandora) brevifrons			
Pandora (Pandora) rachaelae			
Pandora (Pandora) uncifera			
Pandora (Pandorella) granulata			
Pandora (Pandorella) radiata			
Pandora (Pandorella) sarahae			
Frenamya arcuata			
Frenamya cristata			

(Continued)

Table 2. (Continued)

Taxa	Shell Shape	Left Valve Dentition	Right Valve Dentition
Frenamya radians			
Clidiophora claviculata			
Clidiophora cornuta			
Clidiophora dorsorectus			
Heteroclidus punctata			
Foveadens panamensis			
Coania rhypis			

Figures 1–4. **1.** *Pandora brevifrons*, syntype, BMNH 1966572, Panama, sandy bottom, 18 m; length = 22 mm. **2–4.** *Pandora rachaelae* new species, **2.** Holotype, SBMNH 347835, Mexico, Baja California Sur, off Cabo Pulmo, 23°26′00″ N, 109°25′21″ W, 13–17 m; length = 13.9 mm. **3–4.** Paratypes, SBMNH 84939, same locality as holotype; **3.** Length = 14.5 mm, **4.** Length = 14.2 mm.

shallow indentation approximately one-third of total length from anterior end.

Sculpture and Color: Left valve seulpture of commarginal striae and irregular, low commarginal mndulations; left valve with one low radial rib extending from beaks to posterior margin, in some top of rib with granules or nodes; in most, anterior end of left valve demarcated by change in color, without sulcus; right valve sculpture of commarginal striae, with wide commarginal undulations in some, long furrow along posterodorsal margin weak to absent.

Hinge: Left valve with anterior tubercle, and a short obique resilifer; right valve with two cardinal teeth; anterior tooth short, curved in some, not reaching posterior end of anterior adductor musele sear; posterior tooth, thin, elongate, paralleling dorsal margin; lithodesma thin, narrow.

Muscle Scars: Both adduetor muscle scars subcircular.

Lengih: To 14 mm [SBMNH].

Distribution: Los Frailes, Baja California Sur (23.4°N) [SBMNH], to San Felipe, Baja California (31.0° N) [SBMNH], to Puerto Huatulco, Oaxaca (15.8° N) [CAS], Mexico; also at Isla Soeorro, Islas Revillagigedo, Colima, Mexieo (18.8° N) [CAS]; intertidal zone to 60 m, sand [SBMNH].

Type Material: Holotype SBMNH 347835, length = 13.88 mm, height = 6.18 mm, coll. by Carl and Laura Shy, January 1969. Paratypes: SBMNH 84939, same loeality as

holotype, 3 pairs; USNM 1132899, same loeality as holotype, 1 pair. Additional paratypes: CAS 181543, 6 pairs, Mexieo, Colima, Islas Revillagigedo, Isla Socorro, 20 m.

Type Locality: Mexieo, Baja California Sur, off Cabo Pulmo, 23°26′00″ N, 109°25′21″ W, 14–18 m (originally 7–9 fathoms).

Etymology: Named in honor of the senior author's oldest daughter, Raehael Gwinn, in thanks for her continual support and positive attitude.

Comparisons: This species has a more compressed left valve than *P. brevifrons*, has a more ventrally sloping anterodorsal margin, and has a broader, more tubercular anterior eardinal tooth.

Literature and Additional Records: Not seen in previous literature. This species has frequently been misidentified in museum and private collections as *Pandora brevifrons* or *P. granulata*. SBMNH has 13 additional lots.

Pandora (*Pandora*) *uncifera* Pilsbry and Lowe, 1932
(Figure 5)

Pandora uncifera Pilsbry and Lowe, 1932: 104.

Description: Shell Shape: Ellipsoid-elongate; equivalve, both valves compressed, flat; anterior end short; anterodorsal margin eurved ventrally in a distinctive hook; posterior end attenuate, with wide, moderately long, truneate rostrum; ventral margin broadly roumded to straight, except for broad, shallow indentation approximately one-third of length from anterior end.

Sculpture and Color: Anterior end of left valve demarcated by ehange in color, without sulcus, commarginal striae and undulations over entire surface, more subdued anteriorly; left valve with one very low, broad radial rib extending from beaks to posteroventral margin; right valve seulpture of wide commarginal undulations, broad region on posterodorsal margin with vertical striations.

Hinge: Left valve with two eardinal teeth, anterior tooth moderately short, posterior tooth elongate, paralleling dorsal margin; right valve with two weak cardinal teeth, anterior tooth narrow, moderately short, posterior tooth elongate, narrow, resilifer narrow, oblique; lithodesma moderately thiek, narrow.

Muscle Scars: Both adductor muscle scars subcircular to subovate.

Length: To 13 mm [SBMNH].

Distribution: Bahía de las Palmas, Baja California Sur (23.7°N), north to Bahía San Luis Gonzaga, Baja California (29.8°N) [SDNHM, CAS], and Cabo Tepoea, Sonora (30.3°N) [SBMNH], Mexieo, to Manta, Manabí, Ecuador (0.9°S) [PRI]; 5–66 m [SBMNH].

Type Material: Holotype ANSP 155632.

Type Locality: Acapulco, Guerrero, Mexico, 37 m (originally 20 fathoms).

Literature: Gemmell et al. (1987: 61–62), Hertlein and Strong (1946: 97), Keen (1971: 287), Olsson (1961: 454), Pilsbry and Lowe (1932: 104–105).

Subgenus *Pandorella* Conrad, 1863

Pandorella Conrad, 1863. Type species (M): *Pandora arenosa* Conrad, 1834. Miocene, Virginia.
Kennerlia Carpenter, 1864. Type speeies (SD Stoliczka, 1870): *Pandora(Kennerlia) bicarinata* Carpenter, 1864, = *P. bilirata* Conrad, 1855. Recent, California. *Kennerleyia, Kennerlyia, Kenerlyia, Kenerleyia*, of authors, unintentional alterations of an established name.

Description: Hinge of left valve greatly reduced, anterior eardinal tooth a small tubercle or broadly flattened, posterior eardinal tooth absent to reduced. Right valve with two eardinal teeth; anterior small to moderate; posterior short to moderately long. Lithodesma present. External seulpture of right valve with radial grooves or ribs.

Remarks: The dentition of this subgenus is very similar to that of *Pandora s.s.* The prime distinguishing eharacter of *Pandorella* is the presence of radial ribs or grooves in the right valve.

Other eastern Pacifie Ocean species in this subgenus inelude *Pandora* (*Pandorella*) *bilirata* Conrad, 1855, *P.* (*P.*) *filosa* (Carpenter, 1864), *P.* (*P.*) *glacialis* Leach, 1819, and *P.* (*P.*) *wardiana* A. Adams, 1860.

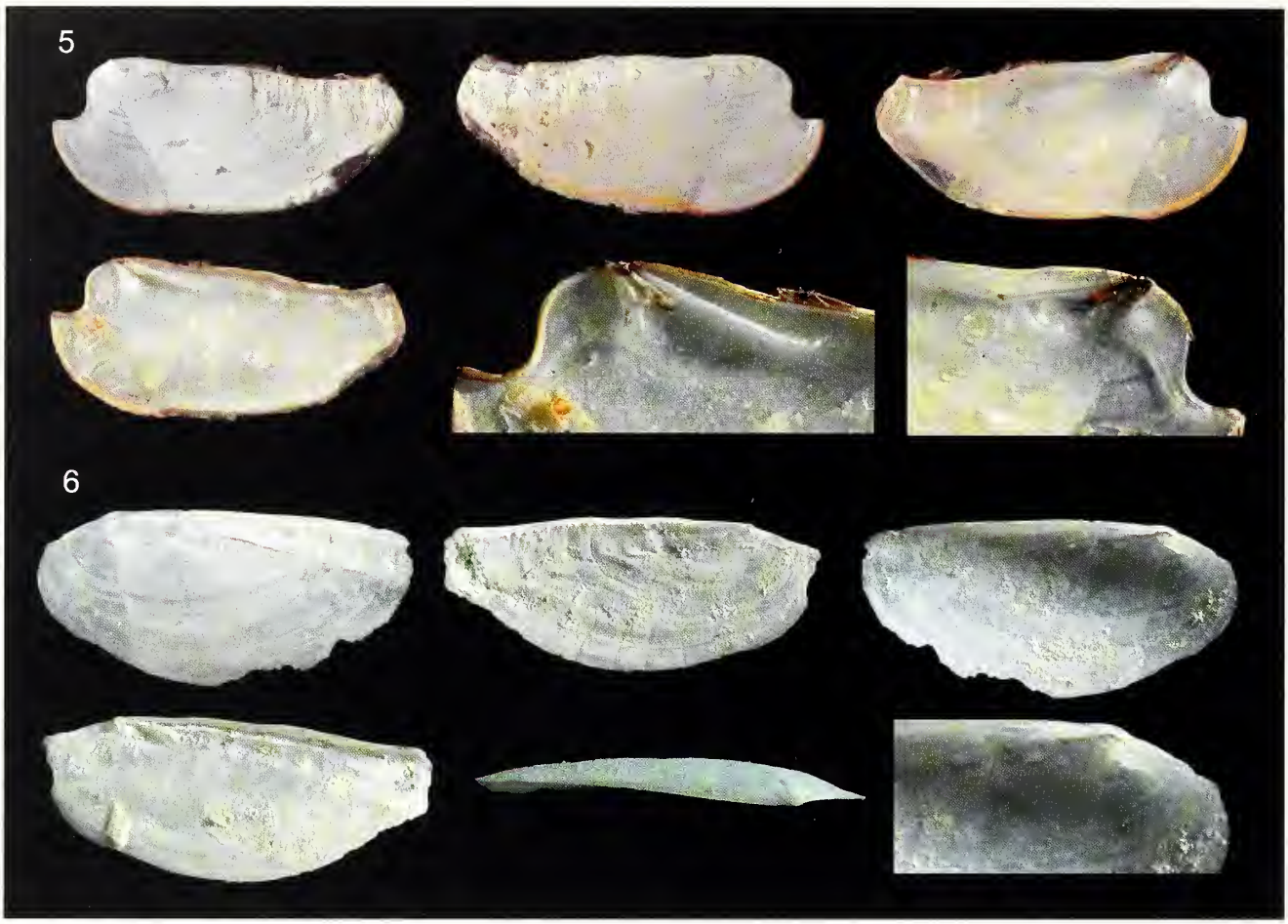
Pandora (*Pandorella*) *granulata* Dall, 1915
(Figure 6)

Pandora granulata Dall, 1915: 449.

Description: Shell Shape: Subquadrate to subovate; inequivalve, left valve moderately inflated, right valve flat to concave; anterodorsal margin straight; anterior end produeed, sharply rounded; posterior end only slightly attenuate, some with very broad, short, subtruncate rostrum; posterodorsal margin straight; right valve overlapping left along posterodorsal margin; ventral margin broadly rounded, with shallow indentation.

Sculpture and Color: Anterior end of left valve demareated by change in sculpture, without sulcus, with a few commarginal undulations on anterior end, central and posterior slopes with commarginal striae only; left valve with two sharp, narrow, radial ribs extending from beaks to posterior margin, with strong commarginal ribs overlying radials forming nodes, granules or scales on some; right valve seulpture of very fine commarginal striae, with few to many (1–10) fine radial grooves that are less prominent or numerous in juveniles.

Hinge: Left valve with one short, obscure anterior cardinal tooth; right valve with two cardinal teeth; anterior



Figures 5–6. **5.** *Pandora uncifera*, SBMNH 347838, Mexico, Baja California Sur, off Cabo Pulmo, 23°26′00″ N, 109°25′21″ W, 13–17 m; length = 13 mm. **6.** *Pandora granulata*, syntype, USNM 211348, Mexico, Baja California Sur, off La Paz, 24°18′ N, 110°22′ W, 48 m; length = 7.2 mm.

short, stout; posterior thin, elongate, paralleling dorsal margin; some right valves with additional internal rib, near end of posterior cardinal, paralleling dorsal margin; ligament narrow, short, oblique; lithodesma broad, stout, short.

Muscle Scars: Anterior adductor muscle sear ovate-elongate, posterior scar subcircular.

Length: To 10 mm [SBMNH].

Distribution: La Paz, Baja California Sur (24.2°N) [USNM], into the Golfo de California as far north as Puerto Libertad, Sonora (29.9°N) [SBMNH], to Teacapán, Sinaloa (22.2°N) [SBMNH], Mexico; 15–80 m [LACM, SBMNH], in sand and mud [SBMNH].

Type Material: USNM 211348, syntypes, about 100 open valves, about 12 closed pairs.

Type Locality: Off La Paz, Baja California Sur, Mexico, 24°18′ N, 110°22′ W, 48 m (originally 26.5 fathoms), broken shell bottom (Albatross 2823).

Remarks: Synonymized in error by Valentieh-Seott (1998) and Coan et al (2000). *Pandora bilirata* Conrad, 1855, has more prominent radial grooves on the exterior of the right valve and does not have granulations on the radial ribs of the left valve.

Literature: Keen (1971: 289).

Pandora (*Pandorella*) *radiata* G.B. Sowerby, 1835 (Figure 7)

Pandora radiata G.B. Sowerby I, 1835: 94; *P.* (*Kennerlia*) *bicarinata* Carpenter, 1864: 638; 1865: 603; *P.* (*Kennerlyia*) *convexa* Dall, 1915: 449.

Description: Shell Shape: Subovate; left valve moderately to highly inflated, right valve flat to very concave, deeply fitting inside left valve; anterodorsal margin with nearly straight slope, slightly upturned on end; posterior end broadly subtruncate, with short broad rostrum in some specimens; posterodorsal margin straight; right valve moderately overlapping left along posterodorsal

margin; ventral margin broadly rounded, with shallow to significant indentation towards anterior end.

Sculpture and Color: Anterior end of left valve demareated by shallow sulcus, entire surface of irregular commarginal striae, some with low, broad, obseure radial ribs; left valve with one narrow radial rib extending from beaks to posterior margin, frequently eroded in larger speeimens, some specimens with faint dorsal rib; right valve seulpture of very fine eommarginal striae, and strong, widely spaeed radial grooves.

Hinge: Left valve with one long, obscure anterior cardinal tooth, in some hinge plate depressed anterior of tooth; right valve with two eardinal teeth; anterior tooth short, stout; posterior tooth thin, elongate, wider ventrally; ligament narrow, moderately short, oblique; lithodesma broad, thiek.

Muscle Scars: Both adductor muscle scars subequal, subeircular.

Length: To 31 mm [USNM].

Distribution: Catalina Island, Los Angeles County, California (33.5°N) [USNM], into the Golfo de California as far north as Isla Smith, Baja California (29.1°N) [SBMNH] and Cabo Lobos, Sonora (29.9°N) [SBMNH], Mexieo, to Zorritos, Tumbes, Perú (3.5°S) [SBMNH]; 20–170 m [SBMNH].

Type Material: *Pandora radiata*: BMNH 1964469, holotype, one pair; *Pandora bicarinata*: USNM 592440, 1 pair mounted on glass slide; Catalina Island, California. *Pandora convexa*: USNM 171068, syntypes, 2 pairs; off lower California, Ballenas, Mexico [Puerto Abreojos, Baja California Sur], 10 m (originally 5.5 fathoms), Albatross 2835, 26°42′30″N, 113°34′15″W.

Type Locality: Insularum Muerte, Columbiae Oeeidentalis [Isla del Muerto, Guayas, Ecuador].

Remarks: The relationship with *Pandora bilirata* Conrad, 1855, should be examined more thoroughly, preferably with moleeular data. It is possible that this northern speeies is a junior synonym of *P. radians*.

Literature: Hertlein and Strong (1946b: 97–98, as *P. convexa*), Keen (1971: 289–291).

Pandora (*Pandorella*) *sarahae* new species
(Figure 8)

Pandora brevifrons G.B. Sowerby I, *of authors, not* G.B. Sowerby I, 1835

Description: Shell Shape: Ellipsoid-elongate; very inequivalve, left valve very inflated, right valve very eoneave; entire shell slightly to moderately twisted dorsoventrally; anterior end short; anterodorsal margin slightly reeurved in most; posterior end attenuate, with short, subtruncate rostrum; ventral margin of left valve straight to slightly rounded, broadly curved along anteroventral and posteroventral margins.

Sculpture and Color: Anterior end of left valve set off by a ehange in seulpture, with commarginal striae anterior of beaks, and fine commarginal ribs posterior of beaks, extending over posterior end, with fine sulcus demareating the two regions; left valve with one moderate radial rib extending from beaks to posterior margin, with heavy commarginal ribs extending across it to the dorsal margin; right valve sculpture of fine commarginal striae, with long, deep, wide furrow along posterodorsal margin, larger speeimens with irregular radial grooves near ventral margin.

Hinge: Left valve with two teeth; anterior tooth low, thiekened tuberele; posterior tooth short, thin, extending anterior of ligament; ligament long, oblique, with thin groove or thickening posterior to it; lithodesma very thin, narrow; right valve with two eardinal teeth; anterior tooth stout, short, curved, not reaching posterior portion of anterior adductor muscle scar; posterior tooth long, thin, paralleling dorsal margin.

Muscle Scars: Anterior adductor musele sear subtrigonal to subeireular, posterior subcircular.

Length: To 12 mm [SBMNH].

Distribution: Bahia Magdalena, Baja California Sur (24.6°N) [SBMNH] and San Felipe, Baja California (31.0°N) [SDNHM], Mexico; 2–10 m, sand [SDNHM, SBMNH].

Type Material: Holotype SBMNH 84940, length = 12.04 mm, height = 5.09 mm. eollected by Carol and Paul Skoglund, October 1979. Paratypes, locality same as holotype: SBMNH 84941, 3 specimens; SBMNH, 2 speeimens; CAS 181988, 1 speeimen, length = 10.63 mm; USNM 1132897, 1 specimen, length = 11.13 mm; Paratypes, SDNHM 90076, Mexico, Baja California, San Felipe, 10 speeimens.

Type Locality: Mexico, Baja California Sur, Bahía Magdalena, Puerto San Carlos, 24°48′7.60″ N, 112°7′17.61″ W, 2–10 m, in sand.

Etymology: Named in honor of the senior author's youngest daughter, Sarah Gwinn, who has a keen biological spirit, and a twisted sense of humor.

Comparisons: No other Panamic pandorid has the strong lateral twisting found in *P. sarahae*. In comparison to *P. grannlata*, *P. sarahae* has a narrower, more produced, anterior end, and fewer radial grooves on the exterior of the right valve. *Pandora radiata* is much wider dorsoventrally than either of the two aforementioned species, and has more, deeper radial grooves in the right valve. *Pandora rachaelae* is not twisted, and most speeimens are compressed.

Literature: Gemmell et al. (1987: 61, as *P. brevifrons*).

Genus *Frenamya* Iredale, 1930

Frenamya Iredale, 1930. Type species (OD): *Coelodon patulus* Tate, 1889. Reeent, Australia.

Figures 7–8. **7.** *Pandora radiata*, holotype, BMNH 1964469, Ecuador, Guayas, Isla del Muerto; length 13 mm. **8.** *Pandora sarahae*, holotype SBMNH 84940, Mexico, Baja California Sur, Bahía Magdalena, Puerto San Carlos, 24°48′7.60″N, 112° 7′17.61″ W, 2–10 m, sand; length = 12 mm.

Coelodon Carpenter, 1865, *non* Audinet-Serville, 1832. Type speeies (SD Stoliczka, 1871): *Pandora ceylanica* G.B. Sowerby I, 1835. Reeent, Ceylon.

Description: Shell strongly inequilateral, posterior end longer; right valve flat to coneave; left valve flat to convex. Hinge of left valve with strong, moderate to long anterior eardinal tooth. Right valve with 3 eardinal teeth, the central cardinal strong, elongate to diamond shaped. Lithodesma absent. External sculpture of commarginal striae or ribs only.

Frenamya arcuata (G.B. Sowerby I, 1835)
(Figures 9–15)

Pandora arcuata G.B. Sowerby I, 1835: 93.

Description: Shell Shape: Ham-shaped; left valve moderately inflated, right valve flat to slightly eoneave, not fitting inside left valve; anterior end relatively short; anterodorsal margin with straight, strong trigonal serrations in most large speeimens; posterior end strongly rostrate; posterodorsal margin moderately to very strongly reeurved, some more reeurved posteriorly; right valve overlapping left along posterodorsal margin, more so near posterior end; ventral margin evenly rounded, almost eireular, without indentation.

Sculpture and Color: Anterior end of left valve demareated by very slight change in eolor, with shallow suleus in some, commarginal striae over entire surface, with one or two very low commarginal undulations in some;

Figures 9–15. **9–14.** *Frenamya arcuata*, syntypes, BMNH 1964467, Ecuador, Guayas, Santa Elena; 9, 13 length = 22 mm; 10 length = 27 mm; 11, 12 length = 25 mm. **15.** *Frenamya arcuata*, SBMNH 119375, Mexico, Baja California Sur, Báhia Santa Maria, 24°44′0″ N, 112°12′ W, 15 fm; length 14 mm.

left valve with one low, broad radial rib extending from beaks to posterior margin, with strong commarginal bars crossing posteriorly; right valve sculpture of very fine commarginal striae, with shallow posterodorsal groove, and rib dorsal to it; right valve without change in color on anterior end.

Hinge: Left valve with three cardinal teeth; anterior tooth long, curved ventrally directed, widest near beaks, ending at the top of the anterior adductor scar; central tooth very small, short, directly below beaks; posterior tooth very thin, moderately long, paralleling dorsal margin; without furrow posterior to ligament; ligament moderately long, broad, oblique; right valve with three cardinal teeth; anterior thin, long, curved, extending to top of anterior end of muscle scar; central tooth moderately short, very stout, diamond shaped, slightly bifid; posterior thick, slightly granulate on top, moderately elongate, paralleling dorsal margin, reaching only half way to posterior adductor muscle scar.

Muscle Scars: Anterior adductor muscle scar subcircular, posterior scar ovate-elongate, posterior scar almost touching dorsal margin.

Length: To 26 mm [SBMNH], reported in literature to 40 mm [Keen, 1971], but no specimens of this length were found.

Distribution: In the Gulf of California as far north as Bahía Santa Maria, Baja California Sur, Mexico (24.7° N) [SBMNH], south to Máncora, Tumbes, Peru (4.1° S) [UMML, CAS]; 15–30 m [SBMNH].

Type Material: BMNH 1964467/1–3, syntypes, 3 left valves.

Type Locality: Ecuador, Guayas, Santa Elena.

Remarks: Unfortunately the type specimens of *F. arcuata* are only left valves, which has led to many misinterpretations of the species. We have found it to be much less common than previously reported.

Olsson (1961: Plate 81, figs. 1a–g) figured a number of species as a single species, and Keen (1971) followed this lead.

The record of *F. arcuata* in Keen (1971) from Laguna Ojo de Liebre, on the Pacific side of Baja California Sur, remains unverified. Specimens of this species were not located from that locality at CAS, which would be the likely repository for specimens that Keen vouchered.

Literature: Carpenter (1865: 596–597), Hertlein and Strong (1946: 98, as *P. cristata*), Hertz et al. (1985), Keen (1971: 287), Olsson (1961: 456).

Frenamya cristata (Carpenter, 1865)
(Figure 16)

Clidiophora cristata Carpenter, 1865: 597

Description: Shell Shape: Subovate-elongate; both valves compressed, twisted to right posteriorly; left valve moderately convex, right valve slightly concave; anterodorsal margin straight, sloping ventrally, some with very weak serrations; posterior end attenuate, with short, truncate, well-demarcated rostrum especially in right valve; posterodorsal margin strongly arcuate; right valve overlapping left along posterodorsal margin; ventral margin broadly rounded, without indentation.

Sculpture and Color: Anterior third of left valve demarcated by change in color, without sulcus, commarginal striae over anterior end; left valve with one heavy broad to narrow radial rib extending from beaks to posterior margin, with shallow groove ventral to it; right valve sculpture of very fine commarginal striae, and irregular low commarginal undulations.

Hinge: Left valve with two cardinal teeth; anterior elongate, narrow, anteroventrally directed towards anterior end of anterior adductor muscle scar; posterior tooth very thin, moderately short, adjacent to the dorsal margin; right valve with three cardinal teeth; anterior elongate, narrow; central tooth short, stout; posterior tooth, elongate, narrow thin, not granulate on top, paralleling dorsal margin; ligament moderately wide, oblique, short; without furrow between ligament and posterior tooth.

Muscle Scars: Adductor muscle scars subequal, anterior subcircular, posterior ovate-elongate.

Length: To 24 mm [BMNH].

Distribution: Only known from the type locality in the Golfo de California, Mexico (general type locality) [BMNH]. Records from Guatemala and El Salvador reported by Hertlein and Strong (1946: 98) remain unverified. Likely these were confused with *P. arcuata*.

Type Material: Holotype BMNH 1963441, 1 pair.

Type Locality: Gulf of California, Mexico.

Frenamya radians (Dall, 1915)
(Figures 17–19)

Pandora (*Coelodon*) *radians* Dall, 1915: 450; *P. arcuata* G.B. Sowerby I, *auctt. non* G.B. Sowerby I, 1835.

Description: Shell Shape: Subovate-elongate; left valve slightly to moderately inflated, right valve flat to slightly concave, fitting inside left valve; anterior end moderate to long; anterodorsal margin with straight to broadly rounded, with strong trigonal serrations in large specimens; posterior end attenuate, with narrow, moderately long, truncate rostrum; posterodorsal margin evenly recurved; right valve overlapping left along posterodorsal margin; ventral margin broadly rounded, without indentation.

Sculpture and Color: Anterior end of left valve demarcated by change in color, without strong sulcus, commarginal striae over entire surface, some with a few commarginal undulations; left valve with one very low, very broad radial rib extending from beaks to posterior margin; right valve sculpture of very fine commarginal striae, with deep posterodorsal groove.

Hinge: Left valve with one long, thin to stout, ventrally directed anterior cardinal tooth, widest near beaks, ending at top of anterior adductor scar; long, narrow furrow posterior to ligament; ligament narrow, oblique; right valve with three cardinal teeth; anterior long, thin; central tooth short, stout, diamond shaped; posterior thin to thick, smooth to granulate on top, very elongate, paralleling dorsal margin, not quite reaching posterior adductor muscle scar.

Muscle Scars: Both adductor muscle scars nearly circular, posterior scar moderately close to dorsal margin.

Length: To 24 mm [SBMNH].

Distribution: Puerto Abreojos, Baja California Sur (26.8° N) [USNM], and Bahía Jolotemba, Nayarit, Mexico (21.4° N) [CAS, Kaiser Collection], to Zorritos, Tumbes, Peru (3.5° S) [Olsson, 1961]; 4–300 m [SBMNH, CAS], mud [SBMNH].

Type Specimens: USNM 171053, holotype, 1 open pair; off lower California, Ballenas, Mexico [Puerto Abrcojos, Baja California Sur], 10 m (originally 5.5 fathoms), Albatross 2835, 26°42′30″ N, 113°34′15″ W.

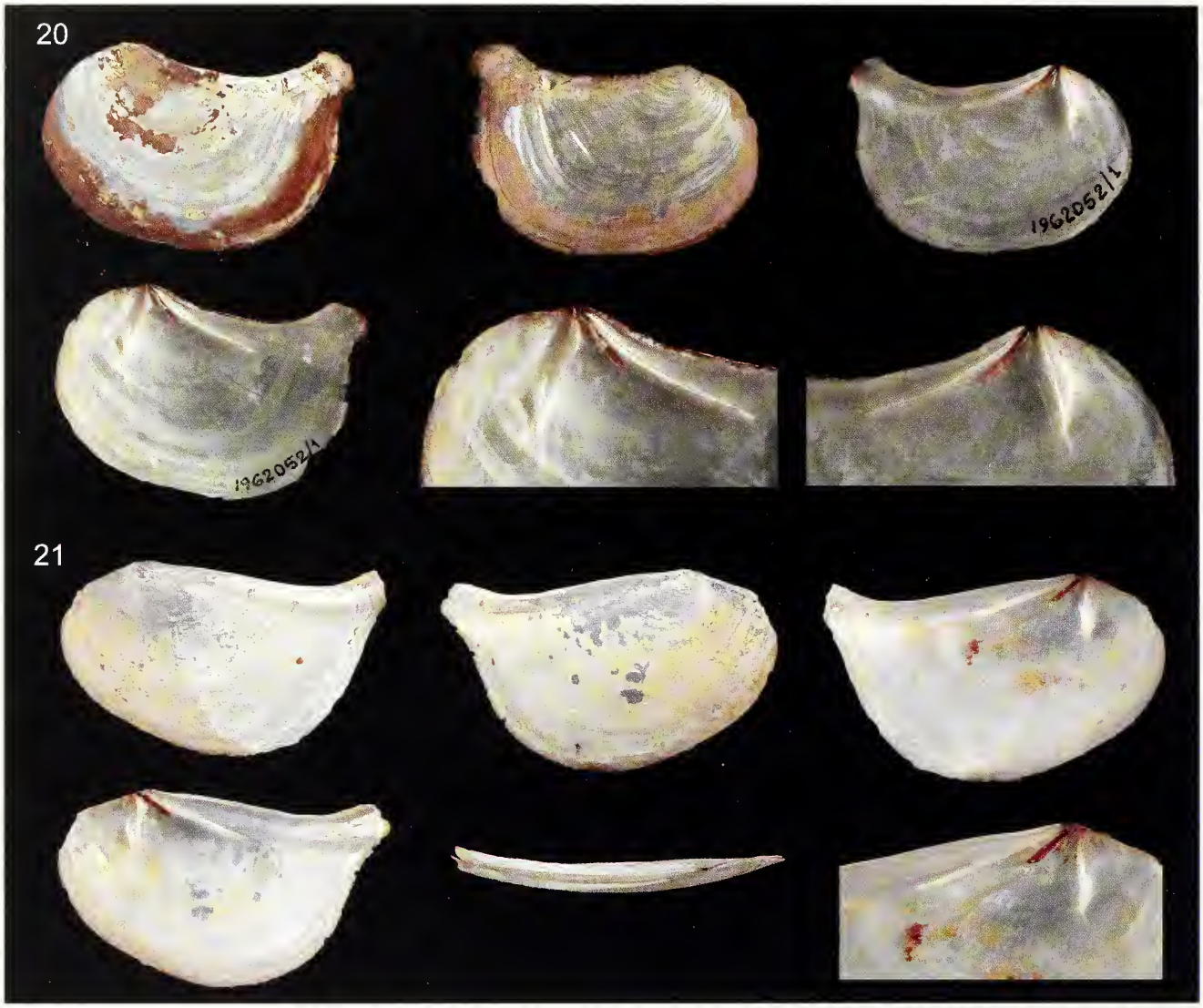
Literature: Dall (1915: 450–451), Keen (1971: 289), Olsson (1961: plate 81, figure 1d as *P. arcuata*).

Genus *Clidiophora* Carpenter, 1864

Clidiophora Carpenter, 1864. Type species (OD): *Pandora claviculata* Carpenter, 1856. Recent, tropical eastern Pacific.

Description: Shell strongly inequilateral, posterior end longer; right valve flat to concave; left valve flat to convex. Hinge of left valve with very strong, long

Figures 16–19. **16.** *Frenamya cristata*, holotype, BMNH 1963441, Mexico, Gulf of California [general locality]; length = 22.5 mm. **17.** *Frenamya radians*, holotype, USNM 171053, Mexico, Baja California Sur, Puerto Abreojos, 26°42′30″ N, 113°34′15″ W, 10 m; length = 15.5 mm. **18–19.** *Frenamya radians*, SBMNH 360635, Mexico, Jalisco, Bahia Tenacatita, Caleta de Los Angeles, 6–20 m; Figure 18, length = 20 mm; Figure 19, length = 24 mm.



Figures 20–21. 20. *Clidiophora claviculata*, syntype, BMNH 1962052, Mexico, Sinaloa Mazatlan; length = 44.5 mm. **21.** *Clidiophora claviculata*, SBMNH 347854, Mexico, Sonora, off Bahía Kino, 28°47′06″ N, 111°57′16″ W, 13 m; length = 45 mm.

anterior cardinal tooth, which ends posterior of the anterior adductor muscle, posterior tooth very long, thin. Right valve with two or three cardinal teeth, the central cardinal very small or absent. Lithodesma present. External sculpture of commarginal striae or ribs only.

Clidiophora claviculata (Carpenter, 1856)
(Figures 20–21)

Pandora claviculata Carpenter, 1856: 228.

Description: Shell Shape: Variable from subovate-elongate to subquadrate; both valves compressed, left valve slightly concave or convex, right valve flat to slightly convex or concave; most specimens twisted to the left; anterodorsal margin straight to curved, rarely with very weak serrations; posterior end broadly rounded to straight, with short, truncate, upturned, well-demarcated rostrum; posterodorsal margin straight to strongly recurved; right valve slightly overlapping left along posterodorsal margin; ventral margin broadly rounded, without indentation.

Sculpture and Color: Anterior half to two thirds of left valve demarcated by change in color in some, without sulcus, commarginal striae over posterior end, becoming more prominent anteriorly, worn specimens with weak radials posteriorly; sculpture of both valves of irregular commarginal undulations and striae; both valves with one heavy broad radial rib extending from beaks to posterior margin, with deep groove ventral to it.

Hinge: Left valve with three teeth; anterior tooth elongate, broad, ventrally directed, ending posterior of

anterior adductor muscle scar; central tooth short to moderate in length, thin; posterior tooth very elongate, narrow, some granulate on top, directed to dorsal portion of posterior adductor muscle scar; ligament narrow, oblique, long; lithodesma broad, long; long, narrow furrow between ligament and posterior cardinal tooth; right valve with two cardinal teeth; anterior tooth moderate to long, narrow dorsally, wide medially, narrow ventrally, sometimes with secondary tooth projecting past middle of anterior adductor muscle scar; posterior tooth thin, very elongate, paralleling dorsal margin, most granulate or serrate on top.

Muscle Scars: Both adductor muscle scars subcircular, posterior scar larger, region dorsal to anterior scar thickened in many.

Length: To 45 mm [BMNH].

Distribution: Laguna Manuela, outer coast of Baja Califorina Sur (28.2°N) [CAS], into the Golfo de California to near its head at San Felipe, Baja California (31.0°N) [SDNHM, SBMNH, CAS] and Puerto Peñasco, Sonora (31.3°N) [SBMNH], south to Mazatlán, Sinaloa (23.2°N) [BMNH], Mexico; 15–60 m [SBMNH].

Type Material: BMNH 1962052/1–3, syntypes, 3 pairs.

Type Locality: Mazatlan, Sinaloa, Mexico.

Remarks: Olsson (1961: 456) and Keen (1971: 287) synonymized *Clidiophora claviculata* with *Frenamya arcuata*. *Clidiophora claviculata* is much more compressed and has the anterior tooth in the left valve directed to the posterior portion of the anterior adductor muscle scar when compared to *F. arcuata*. When compared to *C. cornuta*, *C. claviculata* has a more arcuate posterodorsal margin and a longer rostrum.

Clidiophora claviculata is perhaps the most variable in shell outline of all of the Panamic pandorid species. The type series is very quadrate in overall shape, but commonly specimens we have examined are more ovate-elongate, with a longer rostrum. With further study, it is possible that more than one species might be present in this group. Based on the curvature of the shell and rostrum, this species appears to lay with its right side on the sediment, unlike most other Panamic pandorid species, which lay on their left side.

Literature: Gemmell et al. (1987: 62–63, as *P. cornuta*), Hertz et al. (1985).

Clidiophora cornuta (C. B. Adams, 1852)
(Figures 22–23)

Pandora cornuta C. B. Adams, 1852: 519 [repr.: 295], *ex* Gould ms; *Clidiophora acutedentata* Carpenter, 1865: 598, *nomen vanum* (an unjustified intentional emendation of an established name).

Description: Shell Shape: Subovate; both valves compressed, twisted to left posteriorly; left and right valves slightly convex, right valve slightly concave in some; anterodorsal margin straight and sloping ventrally to slightly curved; posterior end straight to broadly rounded, rostrum short or absent; posterodorsal margin straight, some slightly arcuate terminally; right valve narrowly overlapping left along posterodorsal margin; ventral margin broadly rounded, without indentation.

Sculpture and Color: Anterior half to two-thirds of left valve diagonally demarcated by change in color, without sulcus; left valve sculpture of irregular commarginal striae, with one heavy broad radial rib extending from beaks to posterior margin, without shallow groove ventral to it; right valve sculpture of irregular commarginal striae, with moderately broad groove paralleling dorsal margin; escutcheon absent to long, narrow, shallow.

Hinge: Left valve with three cardinal teeth; anterior tooth elongate, broad, ventrally directed, ending in middle of posterior side of anterior adductor muscle; central tooth very small, short, not well demarcated in small specimens; posterior tooth thin, very elongate, removed from dorsal margin; right valve with two cardinal teeth; anterior tooth short, broad; posterior tooth, elongate, narrow, not granulate on top, removed from dorsal margin; ligament moderately wide, oblique, very long; lithodesma broad, long; with slight furrow between ligament and posterior tooth.

Muscle Scars: Adductor muscle scars subequal, subcircular.

Length: To 36 mm [SBMNH].

Distribution: Laguna Ojo de Liebre, Pacific Coast of Baja California Sur (27.8°N) [SBMNH], into the Golfo de California as far north as San Felipe, Baja California (31.0°N) [SBMNH], and offshore south of Bahía la Choya, Sonora (31.0°N) [CAS], Mexico, to Panamá [MCZ]; intertidal zone to 70 m [SBMNH].

Type Material: MCZ 186309, holotype (broken), 1 pair.

Type Locality: Panama (no specific locality).

Remarks: This species is the most common species found in the museum collections, and perhaps is the most common large species in the Panamic Province. It has been mislabeled in collections as *Pandora claviculata*, *P. panamensis*, and *P. radians*.

Carpenter (1865) renamed this species on the grounds that C. B. Adams' name was misleading, having been based on a broken type specimen that appeared to be "cornuate", e.g. to have posterior horns.

Literature: Hertz et al. (1985), Keen (1971: 289), Olsson (1961: 455).

Clidiophora dorsorectus new species
(Figure 24)

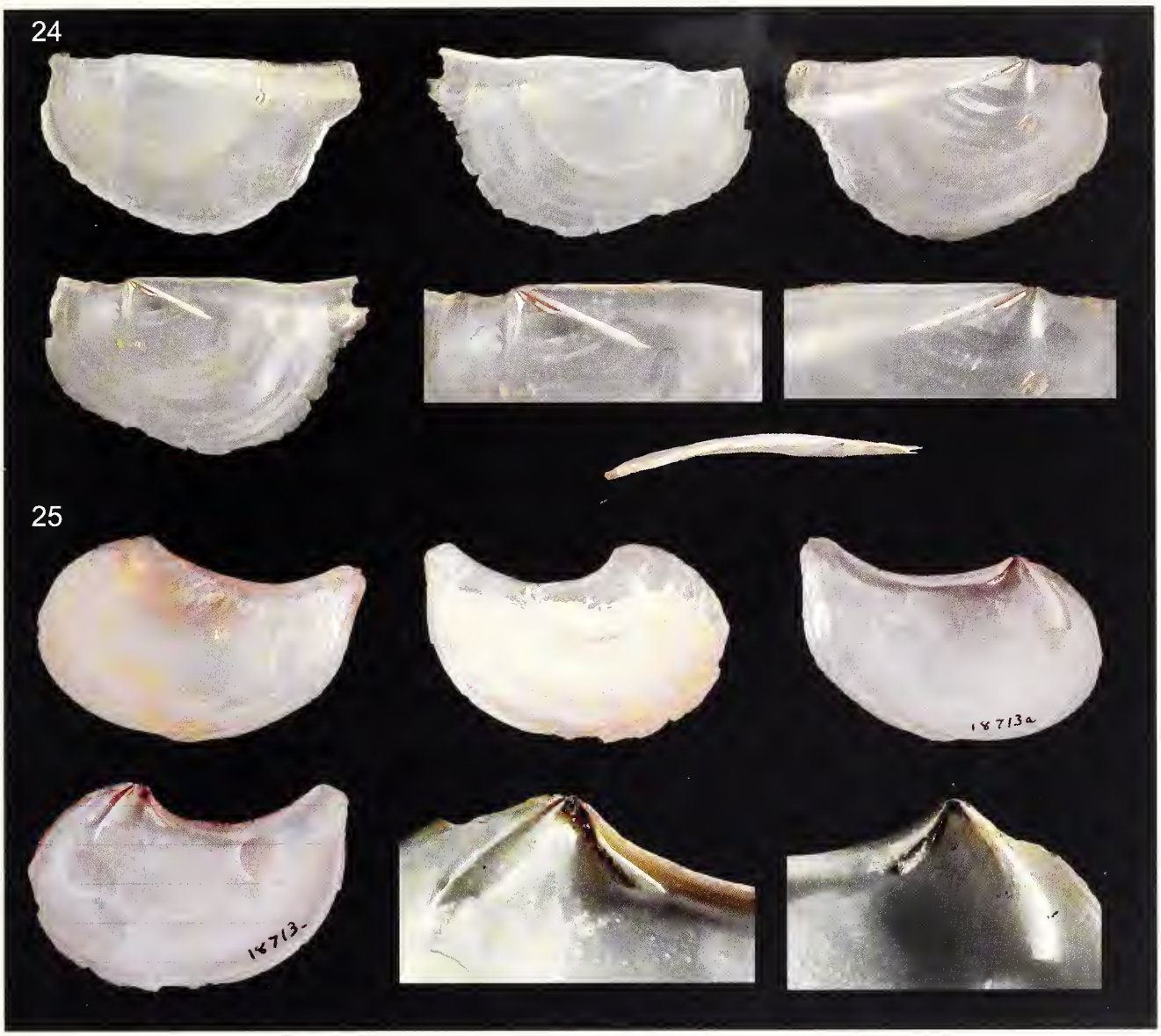
Description: Shell Shape: Subovate-elongate, very fragile, thin, translucent; both valves compressed, left

Figures 22–23. 22. *Clidiophora cornuta*, holotype, MCZ186309, Panama [no specific locality]; length, 16 mm. **23.** *Clidiophora cornuta*, SBMNH 83351, Mexico, Sonora, off Bahia Kino, 28°47′ N, 111°58′ W, 55 m; length = 37 mm.

valve flat to slightly convex, right valve flat to slightly concave; most specimens flat, few twisted slightly to the left; anterodorsal margin straight, not curving ventrally, slightly recurved dorsally, without serrations; posterior end broadly to narrowly rounded, rostrum poorly defined, when visible, short, broad; posterodorsal margin straight; right valve slightly overlapping left along posterodorsal margin; ventral margin broadly rounded, expanded posteriorly, without indentation.

Sculpture and Color: Left valve not demarcated by change in color, without sulcus; sculpture of left valve of commarginal striae and irregular commarginal undulations, stronger posteriorly; left valve with one sharp, broad radial rib extending from beaks to posterior margin, fine commarginal ribs from radial rib to dorsal margin.

Hinge: Left valve with three cardinal teeth; anterior tooth moderately long, moderately broad, ending about one-third of length of the posterior side of the anterior adductor muscle scar; medial tooth short, moderately narrow; posterior tooth thin, very elongate, angling well down from dorsal margin, granulate on top, not quite reaching dorsal end of posterior adductor muscle scar; dorsal to posterior tooth a deep furrow extending from beaks to posterior margin; right valve with two cardinal teeth; anterior tooth short, slightly curved, ventrally directed, ending well short of posterior end of anterior



Figures 24–25. **24.** *Clidiophora dorsorectus*, holotype, SBMNH 83944, Mexico, Baja California Sur, off Punta la Gringa; 29.0321° N, 113.5196° W; 20–40 fathoms [40–80 m]; length = 34 mm. **25.** *Heteroclidus punctata*, SBMNH 118713, California, San Diego County, Coronado Island, intertidal; length = 47 mm.

adductor muscle scar; posterior tooth very elongate, narrow, granulate on top, directed to dorsal portion of posterior adductor muscle scar; ligament long, narrow, oblique; lithodesma broad, thiek.

Muscle scars: Anterior adductor muscle scar subcircular, posterior scar ovate-elongate, region dorsal to anterior sear not thickened.

Length: To 34 mm [SBMMH].

Distribution: In the Golfo de California at Punta la Gringa, Baja California (31.3°N) [SBMNH], and Isla Danzante, (24.7°N) [SBMNH], Baja California Sur, Mexico; 20–90 m [SBMNH].

Type Material: Holotype SBMNH 84944, length = 33.96 mm, height = 19.79 mm, collected by Carol and Paul Skoglund from 1976 through 1993, from type locality. Paratypes, from type locality, SBMNH 84945 (1 specimen); CAS 181987, 1 specimen, length = 21.61 mm; USNM 1132898, 1 specimen, length = 21.12 mm. Paratypes, Mexico, Baja California Sur, west of Isla Danzante, 25.794660°N, 111.281876°W; 30–45 m; collected by Carol and Paul Skoglund, 1984; SBMNH 4 specimens.

Type Locality: Mexico, Baja California, off Punta la Gringa; 29.0321° N, 113.5196° W; 40–80 m (originally 20–40 fathoms).

Etymology: Named after the diagnostic feature – a straight dorsal margin – *dorsorectus*.

Remarks: Like *Pandora claviculata*, this species appears to lay with its right side on the sediment, unlike most other Panamic *Pandora* species, which lay on their left side.

Literature: Not seen in previous literature.

Genus *Heteroclidus* Dall, 1903

Heteroclidus Dall, 1903. Type species (OD): *Pandora punctata* Conrad, 1837. Recent, California.

Description: Hinge of left valve with very strong, long anterior cardinal tooth, which ends anterior of the anterior adductor muscle, posterior tooth very long, thin, paralleling dorsal margin. Right valve with three cardinal teeth, the central cardinal robust, long. Lithodesma present. External sculpture of commarginal striae or ribs only.

Heteroclidus punctata (Conrad, 1837)
(Figure 25)

Pandora punctata Conrad, 1837: 228.
P[andora]. (Heteroclidus) p. gabbi Dall, 1903: 1521.

Description: Shell Shape: Subovate-oblique; both valves compressed, both valves slightly convex, left slightly more convex than right; anterodorsal margin broadly rounded, without serrations; posterior end broadly rounded, with short, truncate, poorly defined rostrum; posterodorsal margin strongly arcuate; right valve overlapping left along posterodorsal margin; ventral margin broadly rounded, with indentation towards anterior slope.

Sculpture and Color: Anterior third of left valve demarcated by change in color and sculpture, with very shallow sulcus, anterior end with irregular commarginal striae and fine granules; posterior two-thirds with commarginal striae; left valve with one very low, broad radial rib extending from beaks to posterior margin, with shallow groove ventral to it; right valve sculpture of very fine commarginal striae, and irregular commarginal undulations.

Hinge: Left valve with two cardinal teeth; anterior tooth elongate, thick, anteroventrally directed; posterior tooth short, narrow, obscure; ligament long, moderately wide, oblique; lithodesma broad, thick, long; right valve with three cardinal teeth; anterior tooth long, narrow; central tooth long, broad; posterior tooth, elongate, narrow.

Muscle Scars: Adductor muscle scars subequal, subcircular; both valves with irregular, widely spaced punctuations dorsal to pallial line.

Length: To 47 mm [SBMNH].

Distribution: Esperanza Inlet, Vancouver Island, British Columbia (49.9°N) [RBCM], to Punta Pequeña, Pacific coast of Baja California Sur, Mexico (26.2°N) [LACM]; subtidal zone to 50 m [SBMNH], in mud. Known from the middle Pliocene of California.

Type Material: BMNH 1966304, possible holotype, 1 left valve.

Type Locality: Santa Barbara, California, USA.

Literature: Carpenter (1865: 598), Coan et al. (2000: 520), Grant and Gale (1931: 262–263), Hertlein and Grant (1972: 336), Keen (1971: 289).

Genus *Foveadens* Dall, 1915

Foveadens Dall, 1915. Type species (OD): *Pandora (Foveadens) panamensis* Dall, 1915. Recent, tropical eastern Pacific.

Description: Hinge of left valve with two short, curved anterior cardinal teeth; posterior tooth long, partially united with the dorsal margin with a septum. Right valve with three cardinal teeth; anterior cardinal small, tubercular; central short, bulbous; posterior elongate. Lithodesma absent. External sculpture of commarginal striae or ribs only.

Foveadens panamensis (Dall, 1915)
(Figures 26–27)

Pandora (Foveadens) panamensis Dall, 1915: 451.

Description: Shell shape: Subquadrate to subovate; both valves very compressed, both valves slightly convex, right slightly more convex than left; anterodorsal margin straight, without serrations; posterior end subtruncate, with short, truncate, poorly defined rostrum; posterodorsal margin straight near beaks, slightly upturned posteriorly; right valve overlapping left along posterodorsal margin; ventral margin broadly rounded, with indentation towards anterior slope.

Sculpture and Color: Anterior third of left valve demarcated by change in color and sculpture in fresh specimens, anterior end opaque, posterior end translucent, with very shallow sulcus, anterior end with irregular commarginal ribs and striae; posterior two-thirds with weak radial and commarginal striae; left valve with one heavy broad radial rib extending from beaks to posterior margin, with shallow groove ventral to it; right valve sculpture of very fine commarginal striae, and irregular commarginal undulations.

Hinge: Left valve with three cardinal teeth; anterior tooth short, stout, trigonal, ventrally directed; central tooth, very short, narrow; posterior tooth elongate, fused to dorsal margin near beaks, forming tunnel between tooth and dorsal margin; ligament moderately wide, oblique, short; without furrow between ligament and posterior tooth; right valve with two cardinal teeth; anterior tooth short, stout, directed towards middle of anterior adductor muscle; posterior tooth, elongate, very thick, sinuous in some; right valve with an additional minute anterior cardinal visible in some specimens.

Muscle Scars: Both adductor muscle scars subovate, posterior slightly larger.

Figures 26–27. 26. *Foveadens panamensis*, holotype, USNM 252276, Panama, "Old Panama," intertidal; length = 19 mm. **27.** *Foveadens panamensis*, SBMNH 83338, Panama, "Old Panama," intertidal; length 23 mm.

Length: To 26 mm [SBMNH].

Distribution: This species is uncommon in collections, known from Ciudad Panamá, Panama (9.0°N) [SBMNH, USNM, UMML], and Archipélago de las Perlas, Panama (approximately 8.5°N) [Olsson, 1961].

Type Material: USNM 252276, holotype, 1 opened pair, badly damaged;

Type Locality: Old Panama, Panama, beach drift.

Literature: Hertlein and Strong (1946: 98), Keen (1971: 289), Olsson (1961: 457).

Coania new genus

Type Species: *Pandora* (*Kennerlia*) *rhypis* Pilsbry and Lowe, 1932: 105.

Description: Hinge of left valve with three cardinal teeth; two moderately short, straight anterior teeth; posterior tooth of moderate length, some slightly united with the dorsal margin with a septum. Right valve with two cardinal teeth; anterior cardinal modertately short, stout; posterior tooth elongate, stout. Lithodesma present. Anterior end of left valve strongly demareated with notch. External sculpture of left valve with radial sculpture centrally and posteriorly; right valve sculpture of fine commarginal striae and weak, irregular radial grooves.

Etymology: Named in honor of Eugene V. Coan, for his tremendous contributions to our understanding of the eastern Pacific Ocean Bivalvia.

Distribution: Thus far only known from the type locality of the type species, in El Salvador.

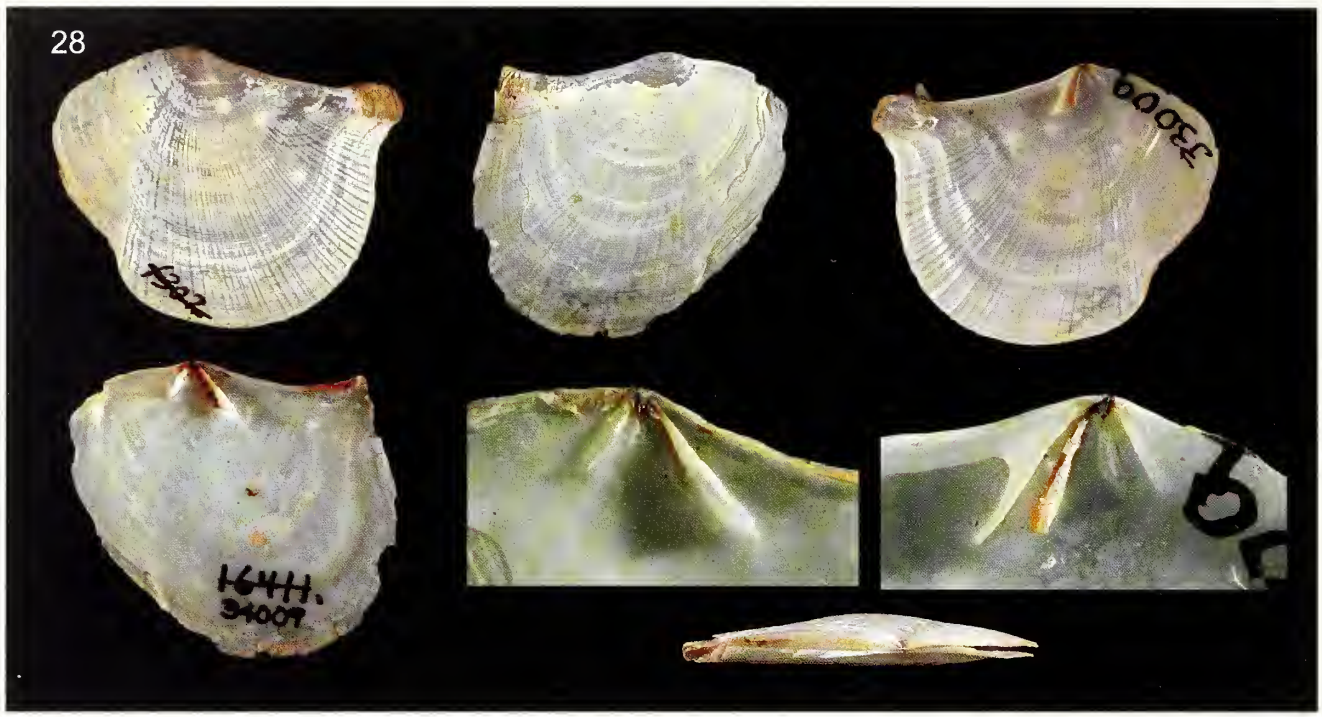


Figure 28. *Coania rhypis*, paratype, SBMNH 39009, El Salvador, La Union, Golfo de Fonseca, La Union; length 24 mm.

Comparisons: The distinct radial sculpture on the left valve and arrangement of the cardinal teeth separate *Coania* from all other genera in the family.

Coania rhypis (Pilsbry and Lowe, 1932)
(Figure 28)

Pandora (Kennerlia) rhypis Pilsbry and Lowe, 1932: 105.

Description: Shell Shape: Subovate-oblique; inequivalve, left valve slightly larger, moderately inflated, right valve flat; anterior end relatively long; anterodorsal margin gently bowed; posterior end very broadly rounded, with short, narrow, truncate rostrum; posterodorsal margin slightly recurved; ventral margin broadly rounded, with deep, broad indentation towards anterior end.

Sculpture and Color: Anterior end of left valve strongly demarcated with noteh, anterior end with irregular commarginal striae, central slope with narrow, moderately spaced radial ribs, becoming obscure posteriorly in some specimens; left valve with two narrow to broad radial ribs extending from beaks to posterior margin; right valve sculpture of very fine commarginal striae, and a few weak, irregular radial grooves, most evident ventrally.

Hinge: Left valve with three cardinal teeth, two teeth anterior of ligament, one longer posterior tooth; ligament narrow, oblique; lithodesma narrow, thin; right valve with two cardinal teeth, moderately elongate, anterior tooth slightly bifid.

Muscle Scars: Anterior adductor muscle scar subeircular, posterior ellipitieal.

Length: To 25 mm [SBMNH].

Distribution: Only known from the type loeality at La Union, Golfo de Fonseca, El Salvador (13.4°N) [SBMNH, ANSP]; 80 m [ANSP].

Type Material: ANSP 155503, holotype, 1 open pair.

Type Locality: La Union, Gulf of Fonseea, El Salvador.

Literature: Keen (1971: 291), Pilsbry and Lowe (1932: 105).

DISCUSSION

Surprisingly little attention has been paid to understanding the taxonomy of members of the Pandoridae, within the Panamic Provinee, as well as globally. They are not an uneommon component of the offshore bivalve fauna. Perhaps it is their fragile, laterally flattened shell that has led to the laek of interest. Or possibly, as we have eneountered, dealing with the variability of shells shapes leads one to give up in disgust. Whatever the reason, we hope that this work will eneourage other bivalve taxonomists to taekle the group in their geographie region.

With 16 pandorid species found in the Panamic Province, one ean postulate that there is likely mueh unexplored diversity in other tropieal and temperate regions around the world. Mikkelsen and Bieler (2007)

only reported three species of *Pandora* from southern Florida, even with extensive offshore collecting. Similarly, Lamprell and Healey (1998), found only two pandorids in all of Australia. Oliver (1992) included two species living in the Red Sea, and further stated that the "Pandoridae is a small group of bivalves. . ." The Chinese coastline includes only three species of pandorids (Valentich-Scott, 2003; Xu, 2004), and only four species are reported from Japanese waters (Okutani, 2000).

We have found the best diagnostic identification characters to be in the hinge, rather than the overall shell shape or inflation. We also suspect if live specimens or wet preserved material becomes available, additional anatomical characters will immediately become apparent. Molecular data will undoubtedly yield further advancement in the understanding of this challenging group of bivalves.

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Descriptions of a new species and a new subspecies of freshwater mussels, *Epioblasma ahlstedti* and *Epioblasma florentina aureola* (Bivalvia: Unionidae), in the Tennessee River drainage, USA

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ABSTRACT

A new species and a new subspecies of *Epioblasma* are described from the Tennessee River drainage, USA. *Epioblasma ahlstedti* (Duck River Dartersnapper) currently is restricted to the Duck River in west-central Tennessee (TN). However, museum collections indicate that the species likely occurred in the Buffalo River, TN, a tributary to the Duck River, and in the Tennessee River at Muscle Shoals, Alabama (AL), and lower Shoal Creek, AL. The following diagnostic morphological characteristics of *E. ahlstedti* are based on the female: (1) pronounced posterior-ventral shell expansion of the adult female shell; (2) slate-gray to dark-purple mantle-pad; (3) spongy texture of the mantle-pad; and (4) display of a single, tan-colored micro-lure that moves slowly side-to-side. *Epioblasma florentina aureola* (Golden Riffleshell) currently is restricted to Indian Creek, a tributary to the upper Clinch River, Virginia. Historically, the species occurred in numerous tributaries in the Tennessee River drainage downstream at least to the Duck River. The following diagnostic morphological characteristics of *E. florentina aureola* are based on the female: (1) gray mantle-pad with a black mottled background; and (2) mantle-pad is pustuled but the pustules are rounded. The genus *Epioblasma* represents the most endangered group of freshwater mussels in North America; 18 of the recognized 25 species or subspecies are already extinct. Likewise, these newly described species and subspecies are critically endangered and despite being listed as endangered under the Endangered Species Act remain in need of focused conservation to prevent their extinction.

Additional keywords: Endangered, molecular DNA markers, phylogenetic analysis, Tennessee River basin

INTRODUCTION

The Tennessee River and its tributaries support the most species-rich mussel assemblage in North America (NA) (Figure 1), with 102 species known historically from the system (Parmalee and Bogan, 1998). Unfortunately, pollution and hydrological modifications (e.g., dams) to the river system over the past 100 years have reduced mussel diversity to approximately 80 extant species (Parmalee and Bogan, 1998; Williams et al., 2008). The decline of species belonging to the genus *Epioblasma* was the most severe (Johnson, 1978). Of the 18 species and subspecies known from the system, only four remain, and of those lost, most are considered extinct and one is extirpated but remains in a small isolated population in Ohio. Species in this genus have specialized reproductive traits, including species with shell morphologies and mantle-lures that can attract and capture their fish hosts to facilitate infestation by the glochidia (Jones et al., 2006; Barnhart et al., 2008). *Epioblasma* shells are characterized by small to medium sizes (~30–70 mm) and sexual dimorphism. The posterior-ventral end of the female shell is expanded, to form a distinct protrusion, or an area of the shell herein termed, the *shell expansion* (Figures 2, 3, 5, 8). This distinctive feature of female *Epioblasma* was considered by Walker (1910) to be the "highest expression of unionid development." The shell expansion houses a modified portion of the mantle, known as the mantle lure that functions to attract host fish. The focal species of the current study belong to the *Epioblasma* subgenus *Torulosa* (Johnson, 1978), which have a prominent shell expansion and a mantle-lure that contains a mantle-pad and micro-lure (Figures 7, 9–14). The mantle-pad is a folded and articulated portion of the mantle, and the micro-lure is a modified and innervated inurrent aperture papilla that moves to attract fish hosts, seemingly mimicking aquatic insect larvae (Jones et al., 2006; Barnhart, 2008).

Such morphological and life history specialization may have contributed to the decline of *Epioblasma* species, as changes in environmental conditions over the 19th and 20th centuries may have disrupted this complex life cycle. Unfortunately, the loss of numerous taxa in the genus has prevented a more complete understanding of the life history and taxonomy of the group, based on modern diagnostic methods using DNA and mantle-lure displays. Since only 7 of the 25 species and subspecies in NA

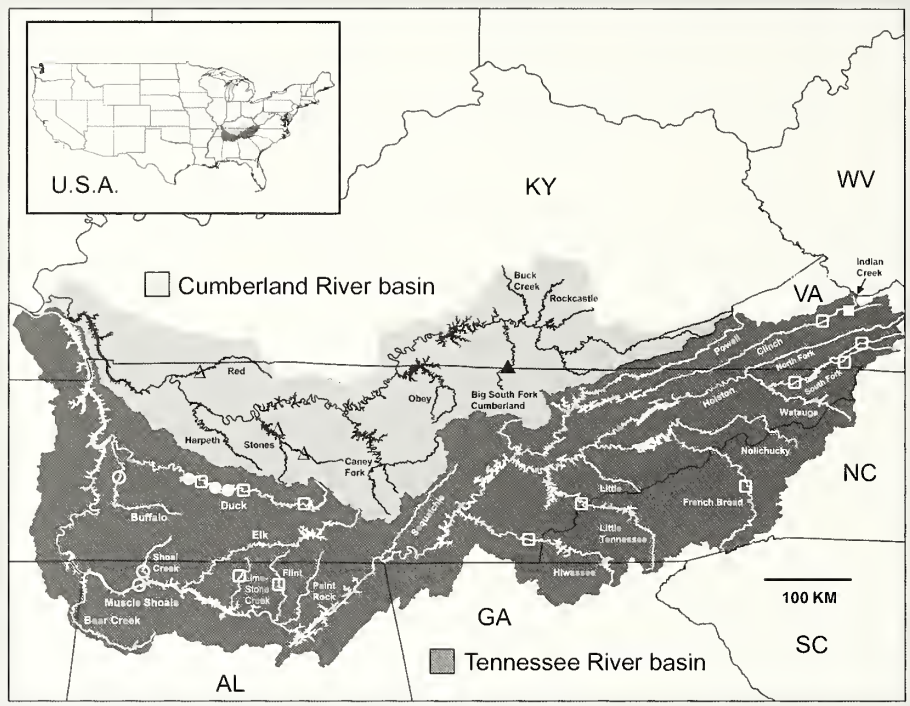

Figure 1. Distribution of *Epioblasma ahlstedti* (current ●, historic ○) and *E. florentina aureola* (current ■, historic □) in the Tennessee River system, USA. Also shown is the distribution of *E. florentina walkeri* (current ▲, historic △) in the Cumberland River system.

remain (Williams et al., 1993), it is possible that additional taxa were never identified before their extinction, while other described taxa may have been phenotypic variants of the same species or subspecies.

The diverse phenotypic variation within *Epioblasma*, especially the varied shell morphologies and mantle-lure displays of females, has allowed for a more comprehensive approach to understanding the taxonomy of extant species within the group, one that includes both traditional phenotypic characters and molecular markers. The study conducted by Jones et al. (2006) showed that the population of *Epioblasma capsaeformis* in the Duck River, Tennessee (TN) was distinct from the population in the Clinch River, TN and Virginia (VA), and that the population of *Epioblasma florentina walkeri* in Indian Creek, VA, a tributary to the upper Clinch River, was distinct from the population in the Big South Fork Cumberland River, TN and Kentucky (KY). Based on extensive phenotypic data (e.g., shell morphology, mantle-lures, fish host specificity) and molecular data (e.g., mitochondrial DNA, nuclear DNA microsatellites), these authors recommended the reclassification of the Duck River and Indian Creek populations of *Epioblasma*, respectively. However, the study did not formally describe and provide taxonomic recognition to these populations. Thus, the purpose of this paper is to present formal descriptions and provide scientific and common names for the new species and new subspecies of freshwater mussel in the Tennessee River system.

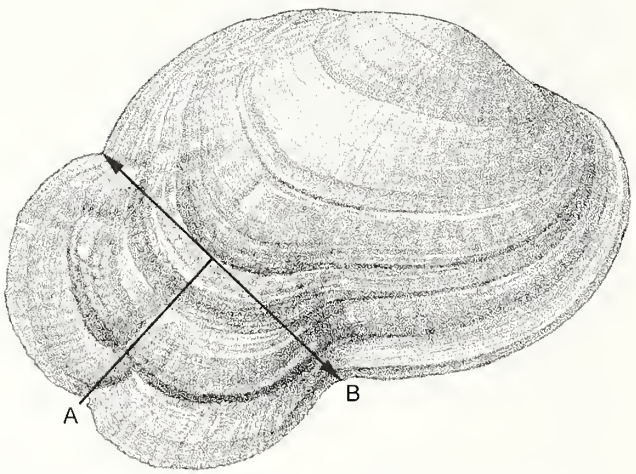

Figure 2. The height (axis-A) and length of the base (axis-B) of the shell expansion are shown. The arrows on axis-B point to the articulation points of the posterior-ventral shell expansion with the main body of the shell. The figure was modified from Burch (1975) and with permission from Dr. J.B. Burch.

MATERIALS AND METHODS

Type specimens, other shell material, and collection records for *Epioblasma ahlstedti*, *E. capsaeformis*, *E. florentina aureola*, *E. florentina florentina* and *E. florentina walkeri* were examined at the following museums: Academy of

Figures 3–4. **3.** Holotype (OSUM 68523) of *Epioblasma ahlstedti* (female), 50.7 mm long and 37.8 mm high; **4.** Paratype (OSUM 82238) of *Epioblasma ahlstedti* (male), 45.8 mm long and 32.0 mm high. Photos by G. Thomas Watters.

Natural Sciences of Philadelphia, Pennsylvania (ANSP); Carnegie Museum, Pittsburgh, Pennsylvania (CM); Florida Museum of Natural History, University of Florida (UF), Gainesville, Florida; Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts (MCZ); Ohio State University Museum of Biological Diversity, Columbus, Ohio (OSUM); and National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM) [see Jones (2004) for all examined lots]. Type specimens provided standard references for comparing shell material from various rivers, and collection records were used to construct species distributions. Museum specimens of *E. ahlstedti* were identified using only female shells.

To assess differences in the shell expansion of adult female shells among populations, simple linear regression equations of total length (x-axis) versus the height (y-axis) of the shell expansion were computed for each population. The height of the shell expansion was measured from its base, which is the length between the two articulation points with the main body of the shell (Figure 2). Digital calipers were used to measure shell dimensions to the nearest 0.1 mm. To test for differences, the slopes of the fitted-lines of each regression equation were compared among populations using the homogeneity of regression coefficients test statistic.

Fecundity was estimated by counting the number of glochidia from each of 6–10 females per population. Although not a diagnostic trait in this study, it helped to demonstrate quantitative differences among species.

Live female mussels for fecundity analysis were collected from the following river locations: (1) *E. ahlstedti*, Duck River, Lillard Mill [River Kilometer (RKM) 287.7], Marshall County (Co.), TN; (2) *E. capsaeformis*, Clinch River between Horton Ford (RKM 321) and Swan Island (RKM 277), Hancock Co., TN; (3) *E. florentina aureola*, Indian Creek, a tributary to the upper Clinch River at RKM 518.2, Tazewell Co., Virginia (VA); (4) *E. f. walkeri*, Big South Fork Cumberland River, Station Camp Creek, Scott Co., TN, downstream to Bear Creek, McCreary Co., KY (Jones et al. 2006).

Figures 5–6. **5.** Holotype (OSUM 82239) of *Epioblasma florentina aureola* (female), 44.1 mm long and 34.8 mm high; **6.** Paratype (OSUM 82240) of *Epioblasma florentina aureola* (male), 48.1 mm long and 33.4 mm high. Photos by G. Thomas Watters.

Fecundity was compared using analysis of variance (ANOVA). All statistical analyses of shells and glochidia were conducted in MINITAB 14 Statistical Software (Minitab, Inc., State College, PA).

Samples of mantle tissue from live mussels were collected from the above river locations and, additionally, individuals of *E. torulosa rangiana* were collected from the Allegheny River, Venango Co., Pennsylvania (PA) (Jones et al., 2006). Other subspecies were not included in the study because they are presumed extinct, i.e., *E. florentina florentina*, *E. florentina curtisi*, and *E. t. torulosa*. A small piece of mantle tissue (20–30 mg) was collected non-lethally from 8–20 live mussels from each population (Naimo et al., 1998).

Sequences of three regions of mitochondrial DNA (mtDNA) and one region of nuclear DNA (nDNA) were amplified by polymerase chain reaction (PCR) using primers and conditions reported in: (1) *16S*, ribosomal RNA (Lydeard et al., 1996) (2) *ND1*, first subunit of NADH dehydrogenase (Buhay et al., 2002; Serb et al., 2003), (3) *cytochrome-b* (Merritt et al., 1998; Bowen and Richardson, 2000), and (4) *ITS-1* (King et al., 1999). All PCR products were sequenced with a Big Dye Terminator Cycle Sequencing kit with Ampli*Taq* DNA Polymerase (Applied Biosystems). Cycle sequence reactions were purified using a Qiagen DNA Purification kit (Qiagene), and subjected to electrophoresis and sequencing using an Applied Biosystems 3100 automated sequencer [detailed PCR methods are available in Jones (2004) and Jones et al. (2006)].

Phylogenetic analysis of DNA sequences and morphological characters were conducted to infer genealogical relationships among *Epioblasma* spp. Sequences from mtDNA and nDNA were combined, and six morphological characters (Table 1) were included in the character matrix for a total evidence analysis (Kluge, 1989). DNA sequences were edited and aligned using the program SEQUENCHER (version 3.0, Gene Codes Corporation), and phylogenetic analysis was performed using PAUP* (version 4.0b10, Swofford, 1998).

Figures 7–14. Mantle-pad displays of female *Epioblasma ahlstedti*, *E. florentina aureola* and congeners. **7.** Mantle-pad and micro-lure of *E. ahlstedti*, Duck River, Marshall Co., TN. **8.** Protruded shell expansion of female *E. ahlstedti*. **9.** *E. capsaeformis* mantle-pad, Clinch River, Hancock Co., TN. **10.** Double micro-lure display of *E. capsaeformis*; **11.** *E. florentina aureola* mantle-pad, Clinch River, Tazewell Co., VA. **12.** Miero-lure of *E. florentina aureola*. **13.** *E. florentina walkeri* mantle-pad and miero-lure, Big South Fork Cumberland River, Scott County, TN. **14.** Pustuled mantle surface of *E. florentina walkeri*. The gaps between shell valves of female mussels are approximately 2 cm. The arrows are pointing at microlures. This figure was previously published in Jones et al. (2006) but updated in this study to inelude the new speeies and new subspecies scientifie names; photograph in Figure 9 has not been previously published. Photographs of the mantle-pad display of *E. torulosa rangiana* are available in Jones (2004).

Table 1. Matrix and coding for shell and mantle-lure characters for *Epioblasma* species. Character states were determined from direct observation and from those reported in Jones et al. (2006). A gap ('–') indicates the character was not applicable to the species.

Species	CHARACTER MATRIX							
	1	2	3	4	5	6	7	8
Epioblasma ahlstedti	1	1	0	0	0	–	1	0
Epioblasma capsaeformis	1	1	0	1	1	–	2	1
Epioblasma florentina aureola	1	1	1	2	2	0	1	0
Epioblasma florentina walkeri	1	1	1	3	2	1	1	0
Epioblasma torulosa rangiana	1	0	2	4	1	–	0	2
Epioblasma brevidens	0	–	–	–	–	–	–	–
Epioblasma triquetra	0	–	–	–	–	–	–	–

CHARACTERS:

(1) Prominent posterior-ventral shell expansion of adult female. 0=absent or diminutive; 1=present.
(2) Denticulations present along margin of posterior-ventral shell expansion. 0=absent; 1=present.
(3) Periostracum color and ray pattern. 0=yellow-green periostracum with irregularly spaced green rays; 1=honey-yellow periostracum with fine green rays evenly spaced over entire shell surface; 2=brown periostracum with irregularly spaced green rays.
(4) Mantle-pad color. 0=dark purple to slate gray; 1=blue to bluish-white; 2=gray with mottled black background; 3=brown with mottled tan background; 4=white.
(5) Mantle-pad texture. 0=spongy; 1=smooth; 2=pustules.
(6) Mantle-pad pustules. 0=rounded; 1=pointed.
(7) Number of micro-lures prominently displayed. 0=0; 1=1; 2=2.
(8) Mantle-pad is invaginated where it meets incurrent aperture. 0=yes; 1=no; 2=incomplete.

Phylogenetic trees were evaluated using the maximum parsimony (MP) criterion because the extent of sequence divergence was low among in-group taxa (Nei and Kumar, 2000; Felsenstein, 2004). Characters were treated as unordered and of equal weight for the analysis due to in-group taxa being closely related (Nei and Kumar, 2000). The tree search was conducted using the branch-and-bound method with ACCTRAN and TBR options; insertions and deletions were treated as missing data. Bootstrap analyses (10,000 replicates) were conducted using the FAST step-wise addition option of PAUP* to assess support for the individual nodes of each phylogenetic tree (Felsenstein, 1985). An additional phylogenetic analysis was conducted using Bayesian inference in MrBayes v3.0b4 (Huelsenbeck and Ronquist, 2001), where the DNA and morphological data sets were combined following the approach of Nylander et al. (2004). MrBayes was run for 1 million generations, sampling trees every 100 generations and posterior probabilities were computed after a burn-in of 40,000 generations. In-group taxa were *E. ahlstedti*, *E. capsaeformis*, *E. florentina aureola*, *E. florentina walkeri*, and *E. torulosa rangiana*. Because of significant differences in morphology and DNA sequences, the Cumberland Combshell (*Epioblasma brevidens*) and Snuffbox (*Epioblasma triquetra*) were designated as out-group taxa. The study by Jones et al. (2006) showed that DNA sequences from these two species are diverged from the in-group taxa by ~5%, and based on obvious differences in shell morphology, Johnson (1978) classified *E. brevidens* and *E. triquetra* into different *Epioblasma* subgenera, *Plagiola* and *Truncillopsis*, respectively. Furthermore, previous phylogenetic studies have demonstrated the monophyly of the *Epioblasma* among North American unionids and that *E. brevidens* and *E. triquetra* are basal to the in-group taxa (Campbell et al., 2005; Zanatta and Murphy, 2006). Thus, available morphological and genetic data justify use of these two species as appropriate out-group taxa.

Photographs of the mantle-pad and micro-lures of live female mussels were taken using a Nikonos V underwater camera with 28 or 35 mm macro-lenses and Kodak 200 Ektachrome film. Female mussels were held in temperature-controlled water in recirculating artificial streams with gravel-filled bottoms. This setup allowed females to display their mantle-pad and behavioral observations of micro-lure movements to be recorded under controlled conditions [photographic methods were previously published in Jones et al. (2006)].

Epioblasma ahlstedti new species
Duck River Dartersnapper
Figures 3, 4, 7, 8

Diagnosis: The following diagnostic morphological characteristics of *Epioblasma ahlstedti* are based on the female and are summarized in Table 2: (1) pronounced posterior-ventral shell expansion of the adult shell; (2) slate-gray to dark purple mantle-pad; (3) spongy texture of the mantle-pad; and (4) display of a single, tan-colored micro-lure that moves slowly side-to-side. In young individuals, the base of the shell expansion is constricted, appearing narrow but distinctly protruded. However, as the female shell grows, the shell expansion becomes extremely protruded and enlarged, compared to the main body of the shell. The shell expansion of *E. ahlstedti* is distinguishable from that of *E. capsaeformis* using the following criteria: (1) length of the shell expansion base in young individuals (~3–5 y), ranging in size from ~35–45 mm, typically appears constricted, being ~5–10 mm narrower basally than those of female *E. capsaeformis* of similar age and size, and (2) mean height (9.6 mm) and maximum height (24.6 mm) of the shell expansion of adult females is significantly greater than that of female *E. capsaeformis* (Table 3; Figure 15).

Description: Length of the female shell can reach 60 to 70 mm, with mean length ~42 mm (Table 3). Male shell lengths are similar. The shell outline of males is typically elliptical, appearing pointed at the posterior end (Figure 4), whereas the shell outline of females is more sub-oval and rounded, with a very enlarged and protruded posterior-ventral shell expansion (Figures 3, 8). The mean height of the shell expansion of the female is ~10 mm or ~23% of shell length, but maximum height is

Table 2. Diagnostic morphological and molecular genetic characters for *Epioblasma ahlstedti*, *E. florentina aureola* and closely related taxa. Data are summarized from Jones et al. (2006).

Species or subspecies	Morphological characters	DNA regions and base-pair site positions	
		mtDNA	nuclear DNA
Epioblasma ahlstedti	• shell expansion of female: large and protruded in adults • mantle-pad color: dark purple to slate-gray • mantle-pad texture: spongy • micro-lure display: 1 lure prominent; rotates clockwise sweeping side-to-side	• *16S*: 2 • *cytochrome-b*: 43, 208, 211, 214 • *ND1*: 281, 564	• *ITS-1*: 152, 153
Epioblasma capsaeformis	• mantle-pad color: blue to bluish-white • mantle-pad texture: smooth • micro-lure display: 2 together; the left lure rotates clockwise, while the right lure rotates counter-clockwise • posterior portion of the mantle-pad is not invaginated where it meets incurrent aperture	• *16S*: 179 • *cytochrome-b*: 13, 87, 148, 184, 327 • *ND1*: 282, 444	• *ITS-1*: 467, 468
Epioblasma florentina aureola	• mantle-pad color: light gray with mottled black background • mantle-pad texture: rounded pustules • micro-lures: 1 lure prominent; rotates clockwise sweeping side-to-side	• *cytochrome-b*: 252 • *ND1*: 405	
Epioblasma florentina walkeri	• mantle-pad color: brown with mottled tan background • mantle-pad texture: pointed pustules • micro-lures: 1 lure prominent; rotates clockwise sweeping side-to-side	• *cytochrome-b*: 52, 96 • *ND1*: 249, 423	• *ITS-1*: 215
Epioblasma torulosa rangiana	• denticulations: absent from posterior-ventral shell expansion • mantle-pad color: white • micro-lures: absent	• *16S*: 167, 452 • *cytochrome-b*: 99, 172 • *ND1*: 30	• *ITS-1*: 44, 127, 385, 386, 387, 388, 511

Table 3. Mean shell length, mean height of shell expansion, and linear regression equations of shell expansion height (y-axis) to total length (x-axis) of adult female mussels. Pairwise comparisons of regression equation slopes were significantly different ($p<0.001$), except equations A vs D, and C vs D. *The p-value indicates the significance level of the slope for each regression equation.

Mussel species	N	Mean length of shell (mm) (range)	Mean height of shell expansion (mm) (range)	Regression equations A–D	R^2	p-value*
Epioblasma ahlstedti	62	41.9 (31.0–68.9)	9.6 (3.1–24.6)	A. $y = -19.8 + 0.701x$	0.76	$p<0.001$
Epioblasma capsaeformis	63	40.7 (30.4–58.4)	8.3 (2.8–14.6)	B. $y = -4.92 + 0.324x$	0.54	$p<0.003$
Epioblasma florentina aureola	55	40.0 (30.7–46.1)	5.7 (1.0–10.2)	C. $y = -16.7 + 0.561x$	0.85	$p<0.001$
Epioblasma florentina walkeri	20	40.5 (30.3–45.2)	8.5 (2.0–14.1)	D. $y = -19.7 + 0.696x$	0.51	$p<0.007$

~25 mm (Table 3), and it is dark green, sometimes appearing almost black. Denticulations occur along the margin of the shell expansion and are typically ~0.5 to 1 mm long and spaced ~0.5 to 1 mm apart. The periostracum of adults is yellowish green, becoming more yellowish at the anterior end. The shell surface contains distinct broad to fine green rays that are typically irregularly spaced. The male shell is short and high with a shallow sulcus. Nacre color is white, but hues of blue and salmon may be present, especially near the beak cavities.

The color of the foot and gills of *E. ahlstedti* is dull white. In females, only the two outer gills are marsupial (i.e., the outer water-tubes contain and brood glochidia when gravid). Located at the distal end of each marsupial water-tube is a pore, which allows for release of glochidia. The mantle-pad is slate-gray to dark purple and has a spongy texture, and the micro-lure is tan (Figure 7). The posterior portion of the mantle-pad is invaginated where it meets the incurrent aperture, so the attachment points of the micro-lures cannot be seen when the female is displaying (Jones et al., 2006).

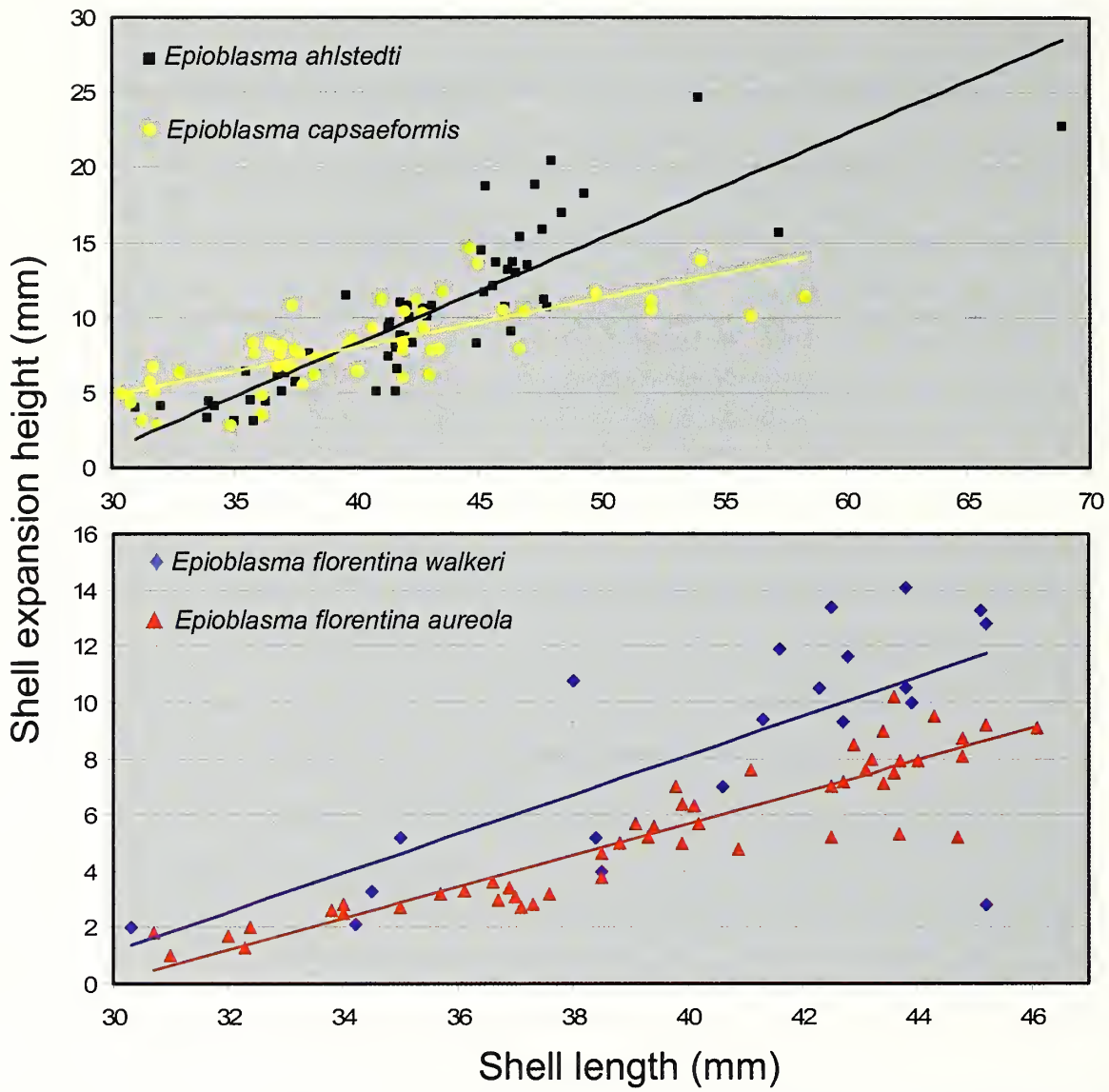

Figure 15. Relationship of posterior-ventral shell expansion height versus shell length of female *Epioblasma ahlstedti* and *E. capsaeformis*, and of female *E. florentina aureola* and *E. florentina walkeri*. Pairwise comparison of regression equation slopes was significantly different ($p<0.001$) between *Epioblasma ahlstedti* and *E. capsaeformis* but not significantly different between *E. florentina aureola* and *E. florentina walkeri*. However, the slope of each regression equation is significant for all four taxa (see Table 3).

Type Material: Holotype: Designated herein as OSUM 68523, collected by H.D. Athearn, from type locality, 30 Sep. 1956. **Paratypes:** CM 61.11669, Duck River, Lillard Mill, Marshall Co., TN, collected by A.E. Ortmann, 25 Aug. 1923; MCZ 236214, Duck River, Lillard Mill, Marshall Co., TN, collected by H.D. Athearn, 30 Sep. 1956; OSUM 52509, Duck River, Lillard Mill, Marshall Co., TN, collected by S.A. Ahlstedt, 1 Oct. 1982; OSUM 82238, Duck River, Lillard Mill, Marshall Co., TN, collected by S.A. Ahlstedt, 1 Oct. 1999 (see Appendix for other material examined); OSUM 82241, Duck River, Lillard Mill, Marshall Co., TN, collected by H.D. Athearn, 30 Sep. 1956.

Type Locality: Duck River, Lillard Mill, Marshall Co., TN, 35°35′09.08″ N; 86°47′14.07″ W.

Comparison with Similar Species: The shell of adult *Epioblasma capsaeformis* (*sensu stricto*) in the Clinch River is of small to medium length (~30–50 mm). The shell surface contains distinct broad to fine green rays that are irregularly spaced, and very similar to those of *E. ahlstedti*. However, the following diagnostic, morphological characteristics of female *E. capsaeformis* distinguish it from *E. ahlstedti*: (1) bluish-white mantle-pad (Figure 9), (2) smooth texture of the mantle-pad, and (3) simultaneous display of two micro-lures that move

Table 4. Fecundity estimates of female *Epioblasma*.

Mussel species	Number of females (*N*)	Mean length (mm)	Length range (mm)	Mean number of glochidia/female	Range
Epioblasma ahlstedti	6	45.4	35.8–56.44	18,757*	6,668–38,716
Epioblasma capsaeformis	10	41.5	36.7–46.4	13,008	7,780–16,876
Epioblasma florentina aureola	7	42.2	40.6–45.7	7,602	3,261–12,558
Epioblasma florentina walkeri	6	42.8	40.5–45.2	9,606	1,828–16,921

*Mean fecundity for *Epioblasma ahlstedti* is significantly different ($p<0.05$) from the other taxa.

synchronously in a circular motion; the left micro-lure moves clockwise, and the right micro-lure moves counterclockwise (Figure 10). The dorsal margin of the mantle-pad is black, forming a discrete uniform band ~2–3 mm wide. The posterior portion of the mantle-pad is not invaginated where it meets the incurrent aperture, so the attachment points of the micro-lures can be seen when the female is displaying. The denticulations along the margin of the shell expansion of *E. capsaeformis* are typically finer and more closely spaced than those of *E. ahlstedti*. The shell expansion is greenish, but not as dark as that of *E. ahlstedti*.

Life History: The typical habitat of *E. ahlstedti* is gravel shoals in medium to large rivers. It is a long-term brooder, gravid from late summer to the following spring and early summer. In the Duck River, at least some females will emerge from the substrate in early spring (e.g., March–April) to display their mantle-pad lure to attract host fishes, while others emerge later in the spring and summer (e.g., May–July). Mean fecundity of females was 18,757 glochidia, and ranged from 6,668 to 38,716 (Table 4). The largest females were not examined; hence maximum fecundity is unknown but likely exceeds 50,000 glochidia. Known fish hosts for *E. ahlstedti* include three darter species, the greenside darter (*Etheostoma blennioides*), fantail darter (*Etheostoma flabellare*), and redline darter (*Etheostoma rufilineatum*) (Jones et al., 2006). However, tested hosts were not collected from the Duck River, but from the North Fork Holston River, VA, in the upper Tennessee River drainage. Although all three darters are widely distributed and common in Duck River, the native Duck River hosts remain uncertain.

Molecular DNA Markers and Phylogenetic Analysis: The Duck River population of *E. ahlstedti* contains presumably diagnostic nucleotides at three mitochondrial DNA gene regions [*16S* (n=1), *cytochrome-b* (n=4), and *ND1* (n=2)] and at one non-coding nuclear DNA region [*ITS-1* (n=2)] (Table 2). Based on analysis of 10 nuclear DNA microsatellite loci, the population is moderately diverged (F_{ST}=0.12) from the Clinch River population of *E. capsaeformis* (Jones et al., 2006). The MP and Bayesian phylogenetic analyses showed high statistical support for the *E. ahlstedti* clade (Figures 16, 17); a finding previously demonstrated by Jones et al. (2006) using only the DNA sequences. Furthermore, the MP tree in Jones et al. (2006) shows *E. ahlstedti* as the basal member of the in-group taxa, whereas the MP tree (Figure 16) reported in this study shows *E. torulosa rangiana* as basal. However, several interior nodes in both MP trees are weakly supported and collapse in the respective consensus trees (not shown). A 50% majority-rule Bayesian consensus tree depicting a more conservative topology is given in Figure 17.

Distribution: *Epioblasma ahlstedti* is currently restricted to 48.3 RKM in the Duck River from Lillard Mill (RKM 286.5) downstream to the backwaters of the Old Columbia Dam reservoir (RKM 238.2) in Marshall Co. and Maury Co., west-central Tennessee (Figure 1). Based on shells, the species likely occurred historically in the Buffalo River, TN (Parmalee and Bogan, 1998), a tributary to the Duck River, and the Tennessee River at Muscle Shoals and Shoal Creek, Lauderdale Co., AL (Jones, 2004).

Conservation Status: The oyster mussel (*Epioblasma capsaeformis*) was listed as endangered under the Endangered Species Act (ESA) in 1997, to include the Duck River population. Now that *E. ahlstedti* has been designated a separate species, it is restricted to only the Duck River population. Being linearly distributed to 48 river kilometers and susceptible to a stochastic impact, this species should be considered critically endangered and continue to receive full protection under the ESA.

Etymology: The species name is given in honor of biologist Steven A. Ahlstedt, U.S. Geological Survey (retired), Knoxville, TN, who has dedicated over 30 years of service to freshwater mussel conservation in the United States. The common name denotes the snapping behavior of many female *Epioblasma* species (i.e., displaying females will quickly close their shells when touched, which can capture a host fish to facilitate infestation with glochidia on the host) (Jones et al., 2006).

Epioblasma florentina aureola new subspecies
Golden Riffleshell
Figures 5, 6, 11, 12

Diagnosis: The following diagnostic morphological characteristics of *E. florentina aureola* are based on the female and are summarized in Table 2: (1) gray mantle-pad with a black mottled background, and (2) mantle-pad has rounded pustules.

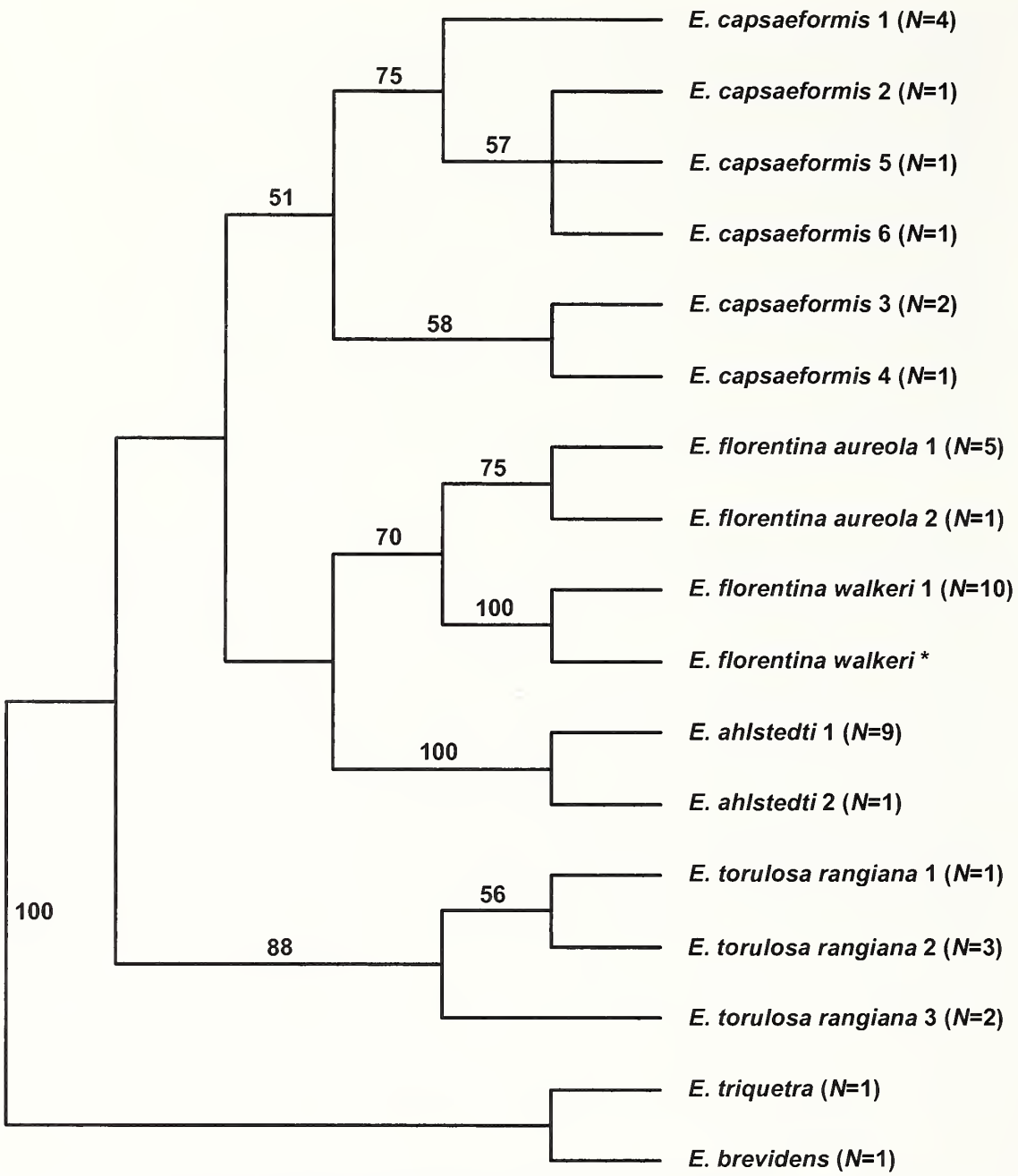

Figure 16. Cladogram showing phylogenetic relationships among *Epioblasma ahlstedti*, *E. florentina aureola* and congeners, inferred from the combined mitochondrial DNA regions of *16S* (468 bp), *cytochrome-b* (360 bp), *ND1* (568 bp), the nuclear DNA region *ITS-1* (515 bp) and eight morphological characters (see Table 1) using maximum parsimony (MP) (31 equally parsimonious trees were resolved; length=195 steps; CI=0.92; RI=0.89). Numbers above the branches (MP) represent bootstrap support (10,000 replicates); only values >50% are shown. All *E. florentina walkeri* were identical; however, to demonstrate the monophyly of this population, an additional sequence was added to the analysis. Out-group taxa are *E. triquetra* and *E. brevidens*.

Description: Length of the female shell can reach 46 mm in Indian Creek and the upper Clinch River, with mean length of 40 mm (Table 3). Shell lengths of males are similar. The shell outline of females is sub-oval and rounded with a moderately protruded shell expansion (Figure 5). The mean height of the female shell expansion is 5.7 mm or ~14% of shell length, but maximum height can reach ~10 mm (Table 3; Figure 15). Dentieulations oeeur along the margin of the shell expansion and are finc and narrowly spaeed ~0.5 mm apart. The shell outline of males is elliptical, appearing pointed at the posterior end (Figure 6), and may have a shallow suleus, especially older individuals. The periostracum of adults can range from golden honey-yellow, to tan and

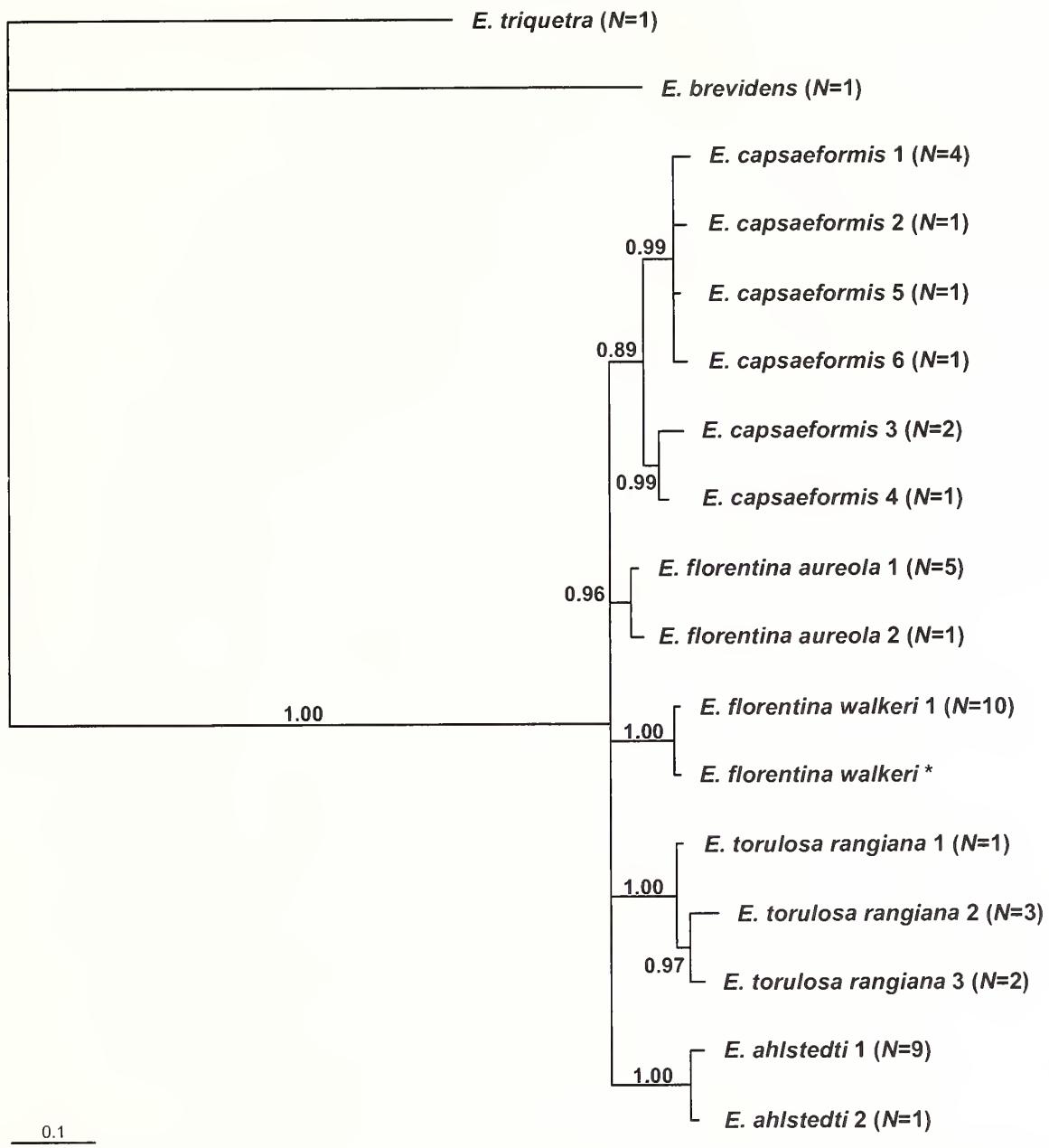

Figure 17. Phylogenetic relationships. **17.** A 50% majority-rule consensus tree (phylogram) showing phylogenetic relationships among the ingroup taxa. The tree was produced from the same DNA sequences and morphological characters listed above and evaluated using Bayesian inference. The analysis was run for 1 million generations with a burn-in of 40,000 generations (mean log likelihood=-3,667). Numbers at the nodes are calculated posterior probabilities (>50%) indicating proportion of trees containing the inferred nodes. Numbers in parentheses at the end of each taxonomic name represent the number of observed DNA haplotypes. *All *E. florentina walkeri* haplotypes were identical; however, to demonstrate the monophyly of this population, an additional sequence was added to the analysis. Out-group taxa are *E. triquetra* and *E. brevidens*.

brown, but coloration is usually evenly distributed over the shell, although occasionally the shell expansion of the female is tinted green. The periostracum contains distinct fine green rays that are evenly spaced over the shell. Nacre color is white, but hues of blue and salmon may be present.

The color of the foot and gills of *E. florentina aureola* is dull white. In females, only the two outer gills serve as marsupia. Each marsupial water-tube contains a distal pore to allow for release of glochidia. The mantle-pad is gray with a black-mottled background and with rounded pustules (Figures 11, 12). The dorsal margin of the mantle-pad is tan, forming a discrete, uniform band ~2–3 mm wide. Micro-lures are darkly colored, and only a single micro-lure is prominently displayed,

which moves slowly side-to-side in a sweeping motion (Figure 12). The posterior portion of the mantle-pad is invaginated where it meets the incurrent aperture, so attachment points of the micro-lures cannot be seen when the female is displaying. The undisplayed microlure is obscured from view inside the invaginated area of the mantle pad (Figure 12).

Type Material: Holotype: Designated herein as OSUM 82239, collected by Leroy Koch, from type locality, 1 Sep. 1998. **Paratypes:** OSUM 16266, Clinch River, Route 460 Bridge, Cedar Bluff, Tazewell Co., VA, collected by D.H. Stansbery and J.J. Jenkinson, 6 Oct. 1965; OSUM 42321, Clinch River, Route 460 Bridge, Cedar Bluff, Tazewell Co., VA, collected by C.R. Ciola, 1 July 1978; OSUM 42434, Clinch River, below railroad bridge, Cedar Bluff, Tazewell Co., VA, collected by C.R. Ciola and G. Wargowsky, 10 Aug. 1978; OSUM 43294, Clinch River, below railroad bridge, Cedar Bluff, Tazewell Co., VA, collected by J.M. Condit and C.R. Ciola, 15 July 1978; OSUM 53252, Clinch River, Cedar Bluff, Tazewell Co., VA, collected by R. Taylor, 10 July 1983; OSUM 82240, Clinch River, Route 460 Bridge, Cedar Bluff, Tazewell County, VA, collected by Leroy Koch, 1 Sep. 1998. (See Appendix for other material examined.)

Type Locality: Clinch River, Route 460 Bridge, Cedar Bluff, Tazewell County, VA, 36°05′16.13″ N; 81°46′05.98″ W.

Comparison with Similar Species: The shell of adult *E. florentina walkeri* (*sensu stricto*) in the Big South Fork Cumberland River is of small to medium length (~30–45 mm) (Table 3), and nearly indistinguishable in shape and color to those of *E. florentina aureola*. The mean height (8.5 mm) and maximum height (14.1 mm) of the shell expansion of adult females is slightly larger than that of female *E. florentina aureola*, but it is not significantly greater (Table 3; Figure 15). The periostracum color of both is honey-yellow, to tan and brown, with fine green rays evenly spaced across the shell. However, the following diagnostic morphological characteristics of female *E. florentina walkeri* distinguish it from *E. florentina aureola*: (1) mantle-pad is brown with a tan-mottled background (Figure 13); and (2) while the mantle-pad also is pustuled, the pustules are pointed and not rounded (Figure 14). The denticulations along the margin of the shell expansion of the female shell are larger and more widely spaced ~1 mm apart, compared to those of *E. florentina aureola*. Similarities include display of a single micro-lure, which moves slowly side-to-side, and the dorsal margin of the mantle-pad is tan, forming a distinctive band ~2–3 mm wide. Similarly, the posterior portion of the mantle-pad is invaginated where it meets the incurrent aperture, so the attachment points of the micro-lures cannot be seen when the female is displaying.

Life History: The typical habitat of *E. florentina aureola* is stable sand and gravel substrates in headwater reaches of rivers and creeks. The subspecies is a long-term brooder, gravid from late summer to the following spring and early summer (Rogers et al., 2001). In Indian Creek, females will emerge in spring and summer (April–July) to display their mantle-pad lure to attract host fishes. Based on an estimate from a single female, maximum fecundity is at least 20,000 glochidia (Rogers et al., 2001). However, mean fecundity based on six females during this study was 7,602 glochidia per female, ranging from 3,261 to 12,558 glochidia (Table 4). Known fish hosts for *E. florentina aureola* based on laboratory trials include: greenside darter (*Etheostoma blennioides*), fantail darter (*E. flabellare*), redline darter (*E. rufilineatum*), snubnose darter (*E. simoterum*), black sculpin (*Cottus baileyi*), mottled sculpin (*C. bairdi*), and banded sculpin (*C. carolinae*) (Jones and Neves, 2001; Rogers et al., 2001).

Molecular DNA Markers and Phylogenetic Analysis: The Indian Creek and upper Clinch River population of *E. florentina aureola* contains presumably diagnostic nucleotides at two mitochondrial DNA gene regions [*cytochrome-b* (n=1), and *ND1* (n=1)] (Table 2). Further, based on analysis of 10 nuclear DNA microsatellite loci, the population is diverged (F_{ST}=0.39) from the Big South Fork Cumberland River population of *E. florentina walkeri* (Jones et al., 2006). The MP and Bayesian phylogenetic analyses showed high statistical support for the *E. florentina aureola* clade (Figures 16, 17), a finding previously reported by Jones et al. (2006).

Distribution: *Epioblasma florentina aureola* is currently restricted to the lower ~1.6 KM of Indian Creek in southwestern Virginia (Figure 1). Historically, this subspecies presumably occurred in numerous tributary streams of the middle and upper Tennessee River system downstream to the Duck River. However, all of these historical populations are considered extirpated. Therefore, the color and texture of the mantle pad and other traits of those populations are unknown. Thus, it is unknown whether these historical populations represented *E. florentina aureola* or other undescribed taxa.

Conservation Status: The Tan Riffleshell (*E. florentina walkeri*) was listed as endangered under the ESA in 1977. Now that *E. florentina aureola* has been designated herein as a separate subspecies, the subspecies only occurs as a single small population in the lower reach of Indian Creek, VA. This subspecies is one of the most critically endangered populations of freshwater mussel in the United States being linearly distributed to a short stream section and highly susceptible to a stochastic event. This subspecies should continue to receive maximum protection under the ESA.

Etymology: The subspecies name *aureola* is the diminutive form of the Latin adjective for golden, and is here chosen to denote the honey-yellow to occasionally golden color of the shell.

Remarks: The anatomical characteristics of females, such as the distal pores, mantle-pad, and micro-lure,

and the shell expansion with denticulations along the margin of the shell are considered advanced traits among unionids, based on their complexity and uniqueness to *Epioblasma* (Jones et al., 2006). The prominent shell expansion of female *E. ahlstedti* is a defining trait first recognized around the turn of the 20th century by the American malacologist Bryant Walker (1856–1936). The following undated letter was written by him and found in a small box in the ANSP shell collection (ANSP 100538). The letter was a hand-written note to a physician and to our knowledge has never been published. The handwriting was difficult to read but was deciphered exactly as is by JWJ, with assistance from Paul Callomon, Elana Benamy, and Earle Spamer of ANSP, on 8 Jan. 2003:

> "I also send some *Truncillas* [*Epioblasmas*] that may be of interest. The Shoal Creek form is typical *eapsaeformis* as I understand it. The male of the Duck R. form is very similar, but the females have invariably the enormous expansion of the specimen sent. In the Clinch, on the other hand, the females are quite typical in form, but the males are usually decidedly more elongated. The Duck R. form has been generally called "*turgidulus*" but it is not. Lea's *turgidulus* is the male of *deviata* as I proved to my own satisfaction, at least, while I was in Washington."
>
> "P.S. The element of uncertainty in *eapsaeformis* matter is the fact that we don't know what the ♀ form of the Cumberland is. The ♀ shell I had at Phila. & which agreed best with Lea's figure of the type was from the Duck R., variety *expansa*. The only Cumberland R. ♀ I have seen is an immature shell belonging to Ferris, and it is apparently like the Tenn. R. & Shoal Crk. form. If the ♀ Cumberland R. form is *expansa* like the Duck R. shell, that would be typical *eapsaeformis* & *expansa* could not be used".

These observations by Bryant Walker indicate that the taxonomic position of the Duck River population was being questioned nearly 100 years ago, and that the expansion of the female shell was seen as a diagnostic trait when compared to specimens collected from other rivers in the region, including shells from the Clinch River. In Walker's view, the size of the shell expansion of adult females is a signature phenotypic character, reaching a mean and maximum height that is greater than those of other species and subspecies belonging to the *Epioblasma* subgenus *Torulosa* [*sensu* Johnson (1978)]. Thus, the combination of key phenotypic traits, especially the unique shell morphology and mantle-lure display of females, unambiguously define *E. ahlstedti* as a valid species.

The population of *Epioblasma florentina aureola* in the upper Clinch River watershed is not deserving of a separate species designation because of several shared traits with *E. florentina walkeri* in the Big South Fork Cumberland River: (1) honey-yellow to tan-colored periostracum, (2) similar fish host specificity, (3) pustuled mantle-pads, and (4) preference for headwater stream habitats. These two populations also have similar-sized glochidia, similar fecundity, and are closely related phylogenetically. In addition, the periostracum color of the nominal species *E. florentina florentina* is also yellow and was thought to simply represent clinal variation; i.e., the large river form of the subspecies complex. Ortmann (1918; 1924; 1925) considered the two forms as merely clinal variants, a claim supported by his observation that the big river form appeared to grade into the headwater form as one progressed upstream. However, based on the shell material examined in Jones (2004) and Jones et al. (2006), it is uncertain whether *E. florentina florentina* merely represents clinal variation, a subspecies or perhaps even a separate species for the following reasons: (1) large distances of seemingly unoccupied habitat commonly occurred between mainstem and headwater populations (e.g., Clinch and Holston rivers >200 RKM), and ecological conditions between mainstem and headwater locations are substantial (e.g. distribution of host fishes, water temperature, stream size, etc.); (2) a transitional series of shells representing a continuously distributed population of this species from mainstem to headwaters *does not exist*; and (3) because most populations are extirpated, additional genetic, morphological and life history data are unobtainable. For example, available specimens of *E. florentina florentina* collected from the lower Clinch River near its mouth are short (~30–35 mm), solid, and thick-shelled, and are quite distinctive from the larger-sized headwater form *E. florentina aureola* (Jones, 2004). However, because *E. florentina florentina* is extinct, adequate comparisons of the mantle-lure and DNA cannot be made with the other subspecies. Therefore, since each nominally described subspecies occurred or occurs in distinct geographic regions and habitats, we believe *E. florentina* ssp. minimally was a polytypic species complex and best categorized by the current trinomial designations.

The current taxonomy of *Epioblasma* recognizes 20 species and 5 subspecies (Turgeon et al., 1998; Williams et al., 1993). Thus, with the description of *E. ahlstedti* and *E. florentina aureola*, 21 species and 6 subspecies now are recognized in the genus. The historical distributions of *E. florentina aureola* and *E. florentina walkeri* are unclear because most populations are extirpated and only shell material and collection records are available to assess the distribution of each subspecies. Furthermore, the anatomy of live individuals cannot be compared among historical populations. Therefore, a practical approach to delineating the distribution of each subspecies is to consider all records of *E. florentina walkeri* in the Tennessee River drainage as *E. florentina aureola*, and all respective records in the Cumberland River drainage as *E. florentina walkeri*. This approach would simplify the management and recovery of each subspecies within their respective river drainages.

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APPENDIX 1. Shell collection lots of *Epioblasma ahlstedti* and *E. florentina aureola* examined during this study are provided below, where NA=Not Available, H=holotype, P=paratype.

The following lots are of *E. ahlstedti*:

Museum	Lot number	Type	Location	Collector	Date
ANSP	100504		Duck River, TN	H.H. Smith	NA
ANSP	100538		Shoal Creek, Lauderdale Co., AL	H.H. Smith	NA
ANSP	391133		Duck River, Hardison Mill, Maury Co., TN	S. Ahlstedt	1/16/1986
CM	61.646		NA	Hartman Collection	NA
CM	61.4491		Shoal Creek, Lauderdale Co., AL	B. Walker	11/2/1909
CM	61.6498		Shoal Creek, Lauderdale Co., AL	A.E. Ortmann	NA
CM	61.7696		Tennessee River, Florence, Lauderdale Co., AL	A.E. Ortmann	NA
CM	61.7697		Shoal Creek, Lauderdale Co., AL	A.E. Ortmann	NA
CM	61.11267		Duck River, Maury Co., TN	A.E. Ortmann	8/26/1921
CM	61.11497		Duck River, Maury Co., TN	A.E. Ortmann	9/6/1922
CM	61.11669	P	Duck River, Lillard Mill, Marshall Co., TN	A.E. Ortmann	8/25/1923
CM	61.11670		Duck River, Wilhoite, Marshall Co., TN	A.E. Ortmann	8/27/1923
CM	61.11672		Duck River, Leftwich, Maury Co., TN	A.E. Ortmann	9/3/1923
UF	64238		Tennessee River, Florence, Lauderdale Co., AL	A.A. Hinkley	1904
UF	64241		Duck River, Wilhoite, Marshall Co., TN	NA	NA
UF	64242		Duck River, Hardison Mill, Maury Co., TN	NA	NA
UF	64245		Tennessee River, Muscle Shoals, Lauderdale Co., AL	H.H. Smith	11/1/1909
UF	64250		Shoal Creek, Lauderdale Co., AL	H.H. Smith	10/1/1909
UF	226003		Duck River, TN	NA	NA
UF	269045		Duck River, Columbia, Maury Co., TN	A.A. Hinkley	NA
UF	269049		Duck River, TN	Marsh	NA
UF	269058		Duck River, Columbia, Maury Co., TN	B. Walker	NA
MCZ	6210		Duck River, Columbia, Maury Co., TN	R.E. Call	NA
MCZ	29828		Shoal Creek, Lauderdale Co., AL	B. Walker Collection	NA
MCZ	83995		Duck River, Wilhoite, Marshall Co., TN	Goodrich	NA
MCZ	83441		Shoal Creek, Lauderdale Co., AL	H.H. Smith	NA
MCZ	236214	P	Duck River, Lillard Mill, Marshall Co., TN	H.D. Athearn	9/30/1956
MCZ	236718		Tennessee River, Musele Shoals, Lauderdale Co., AL	B. Walker Collection	NA
MCZ	272794		Duck River, Maury Co., TN	P. Yokley	9/3/1965
OSUM	8628		Duck River, TN	NA	1800's
OSUM	12246		Duck River, 431 Bridge, Maury Co., TN	C.B. Stein	7/19/1964
OSUM	14496		Duck River, Sowell Ford, Maury Co., TN	P. Yokley	7/7/1965
OSUM	14864		Duck River, Milltown, Marshall Co., TN	D.H. Stansbery	9/5/1964
OSUM	15149		Duck River, Wilhoite Mill, Marshall Co., TN	D.H. Stansbery	9/8/1964
OSUM	16229		Duck River, Sowell Ford, Maury Co., TN	P. Yokley B. Isom	9/2/1965
OSUM	16238		Duck River, Columbia, Maury Co., TN	P. Yokley B. Isom	9/1/1965
OSUM	33341		Duck River, Milltown, Marshall Co., TN	D.H. Stansbery W.J. Clench	10/14/1972
OSUM	33922		Duck River, Wilhoite Mill, Marshall Co., TN	P. Yokley B. Isom	9/3/1965
OSUM	33959		Duck River, Milltown, Marshall Co., TN	P. Yokley B. Isom	9/3/1965
OSUM	34074		Duck River, Leftwich, Maury Co., TN	P. Yokley B. Isom	9/3/1965
OSUM	50107		Duck River, TN	NA	Prior 1931
OSUM	50108		Duck River, TN	NA	Prior 1928
OSUM	52509	P	Duck River, Lillard Mill, Marshall Co., TN	S. Ahlstedt	10/1/1982
OSUM	57291		Duck River, TN	Wheatley	Prior 1882
OSUM	67899		Duck River, Shelbyville, TN	Call	1885

(Continued)

APPENDIX
(Continued.)

Museum	Lot number	Type	Location	Collector	Date
OSUM	68523	H	Duck River, Lillard Mill, Marshall Co., TN	H.D. Athearn	9/30/1956
OSUM	82238	P	Duck River, Lillard Mill, Marshall Co., TN	S.A. Ahlstedt J. Powell	10/1/1999
OSUM	82241	P	Duck River, Lillard Mill, Marshall Co., TN	H.D. Athearn	9/30/1956
USNM	510913		Duck River, Columbia, TN	NA	NA
USNM	521353		Duck River, Columbia, TN	NA	NA

The following lots are of *E. florentina aureola*:

Museum	Lot number	Type	Location	Collector	Date
ANSP	103740		Flint River, Maysville, AL	H.H. Smith	NA
ANSP	103903		Hurricane Creek, Gurley, AL	H.H. Smith	NA
ANSP	103997		Flint River, Gurley, AL	H.H. Smith	NA
CM	61.6765		South Fork Holston River, Washington Co., VA	A.E. Ortmann	NA
CM	61.6767		South Fork Holston River, Emmitt, Sullivan Co., TN	A.E. Ortmann	NA
CM	61.11668		Duck River, Wilhoite, Marshall Co., TN	A.E. Ortmann	NA
UF	269050		Flint River, Madison, Co., AL	B. Walker	NA
UF	269057		Tennessee	C.T. Simpson	NA
UF	269059		Tennessee	NA	NA
MCZ	276026		Middle Fork Holston River, Route 91 Bridge, Smyth Co., VA	Wilson & Clark	8/21/1911
MCZ	293653		Middle Fork Holston River, Chilhowie, Smyth Co., VA	R.E. Winters	9/2/1977
OSUM	15150		Duck River, Wilhoite Mills, Marshall Co., TN	D.H. Stansbery	9/8/1964
OSUM	16266	P	Clinch River, Route 460 Bridge, Cedar Bluff, Tazewell Co., VA	D.H. Stansbery & J.J. Jenkinson	10/6/1965
OSUM	16344		Clinch River, Route 80 Bridge, Russell Co., VA	D.H. Stansbery & J.J. Jenkinson	10/6/1965
OSUM	24342		Middle Fork Holston River, Route 91 Bridge, Smyth Co., VA	D.H. Stansbery & W.J. Clench	9/16/1968
OSUM	25330		Middle Fork Holston River, Route 638 Bridge, Smyth Co., VA	D.H. Stansbery	8/28/1970
OSUM	29072		Duck River, Route 65 Bridge, Maury Co., TN	S.A. Ahlstedt	4/26/1988
OSUM	34943		Middle Fork Holston River, Chilhowie, Smyth Co., VA	D.H. Stansbery	10/16/1973
OSUM	42198		Middle Fork Holston River, Route 638 Bridge, Smyth Co., VA	D.H. Stansbery & F.L. Kokai	7/24/1978
OSUM	42321	P	Clinch River, Route 460 Bridge, Cedar Bluff, Tazewell Co., VA	C.R. Ciola	7/1/1978
OSUM	42434	P	Clinch River, below railroad bridge, Cedar Bluff, Tazewell Co., VA	C.R. Ciola & G. Wargowsky	10/8/1978
OSUM	43294	P	Clinch River, below railroad bridge, Cedar Bluff, Tazewell Co., VA	J.M. Condit & C.R. Ciola	7/15/1978
OSUM	53252	P	Clinch River, Cedar Bluff, Tazewell Co., VA	R. Taylor	7/10/1983
OSUM	57118		French Broad River, Asheville, Buncombe Co., NC	J.F. Hardy	NA
OSUM	82239	H	Clinch River, Route 460 Bridge, Cedar Bluff, Tazewell Co., VA	L. Koch	9/1/1998
OSUM	82240	P	Clinch River, Route 460 Bridge, Cedar Bluff, Tazewell Co., VA	L. Koch	9/1/1998
USNM	29898		French Broad River, Asheville, NC	NA	NA

New species of *Bolma* (Gastropoda: Vetigastropoda: Turbinidae) from the tropical deep sea

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ABSTRACT

Five new species of *Bolma* are described, three from New Caledonia, one from Mozambique and one from French Polynesia, all from deep reef (75–155 m) to bathyal (230–580 m) depths. Four of the new species have been sequenced, and their holotypes are also voucher specimens for COI sequences, thus contributing to a new generation of name-bearing types. The descriptions and names are provided in advance of a forthcoming shell-based revision of the genus *Bolma*, and in advance of a detailed molecular- and morphology-based study of *Bolma* in New Caledonian waters.

INTRODUCTION

The gastropods of the turbinid genus *Bolma* Risso, 1826, live at tropical and warm-temperate latitudes in the Mediterranean, West African, South African, and Indo-West Pacific biogeographical provinces; there are no *Bolma* in the western Atlantic or eastern Pacific. With the exception of the type species *Bolma rugosa* (Linnaeus, 1767), which occurs commonly near-shore to about 200 meters deep, *Bolma* species are uncommon to rare, mostly on hard bottoms between 100 and 500–800 meters deep. Beu and Ponder (1979) revised the Recent and fossil species, and recognized 19 valid species (two of which with, respectively, 2 and 3 subspecies), from among 29 nominal species. Ongoing explorations have since added 12 more species, all from South Africa and the Indo-West Pacific. Some of the taxa treated by Beu and Ponder as synonyms or subspecies have also been re-evaluated, and the genus *Bolma*, with about 35 valid species, is the subject of a forthcoming monograph by Axel Alf and Kurt Kreipl, to appear in the *Conchological Iconography*. The purpose of the present paper is to describe several new species prior to the publication of that monograph. Three of them originate from New Caledonia, which has been intensively sampled since the late 1970s through the Tropical Deep-Sea Benthos program (Bouchet et al., 2008). Early in the program, Bouchet and Métivier (1983) reported three species of *Bolma* from New Caledonia, namely *B. guttata* (A. Adams, 1863), *B. lienica* (Watson, 1885), and *B. opaoana* Bouchet and Métivier, 1983. Since then, the program has been extended to other island groups in the South Pacific and, more recently, in the Indian Ocean, revealing still more species of *Bolma*. One of the new species is thus described based on material collected from seamounts surveyed off Madagascar in 1980, and then again off Mozambique in April 2009. And finally, while this paper was being put together, another very distinctive new species was collected in September–October 2009 off the Society Islands in French Polynesia.

One difficulty of *Bolma* systematics—in common with other vetigastropods with their non-feeding short-lived planktonic larvae—is the understanding of what constitutes geographical vs. population variation (Meyer et al. 2005). In this respect, the Bolmas of New Caledonia and the Solomon Islands have been the subject of molecular work by Magalie Castelin, as part of her Ph.D. thesis, the results of which will be reported elsewhere. The purpose of the present paper is also to provide names and facilitate the presentation and discussion of this molecular work.

Abbreviations and Text Conventions: lv, live-taken specimen; dd, empty shell; stn, station; MNHN, Muséum National d'Histoire Naturelle, Paris, France; NMNZ, Museum of New Zealand Te Papa, Wellington, New Zealand; NMP, Natal Museum, Pietermaritzburg, South Africa; ZRC, Raffles Museum, Zoological Reference Collection, National University, Singapore.

SYSTEMATICS

Family Turbinidae Rafinesque, 1815
Genus *Bolma* Risso, 1826
Type Species: *Turbo rugosus* Linnaeus, 1767 (by monotypy).

Bolma castelinae new species
(Figures 1–7)

Description: Shell of average size for genus, trochoid with straight sides, as tall as wide, spire angle about 75°,

rather thin-shelled and light. Teleoconch of 6¾ whorls, first two planispiral, subadult and adult whorls convex with angular peripheral cord overhanging narrow, flat, subsutural ramp, giving the impression of deep suture. Basal cord delimiting distinct basal disc. Sculpture consisting of beaded spiral cords, number of cords increasing from single subsutural cord above periphery on third whorl, to 3 on last 3 whorls, and with 3 additional secondary cords on last 1/3 whorl behind aperture; strong peripheral and weaker basal cords bearing short, scaly spines; space between peripheral and basal cords almost vertical, overall smooth except for one cord bearing short, scaly spines; base smooth, polished. Columella smooth and evenly rounded, thickened, but basal callus indistinct. Aperture oval, outer lip sharp in holotype (expanded in fully adult specimens). No umbilicus. Background color pinkish salmon, beads, adapertural side of spines, and interspace between peripheral and basal cords lighter, base porcellaneous white; columella white and nacreous, aperture nacreous within. Operculum thick, convex, smooth, white. Dimensions of holotype: height 25.2 mm, diameter 25.1 mm. Adults may reach a height of 30 mm, diameter 28 mm.

Holotype: MNHN 22823 (lv).

Paratypes: 1, MNHN 22824 [Ebisco, stn CP2579, 20°21′ S, 158°40′ E, 440–455 m, 1 Oct. 2005]; 1, MNHN 22840 [Halical 1, stn DW02, 18°54′ S,. 163°24′ E, 352–397 m, 23 Nov.1994]; 1, ZRC.MOL.2954 [Smib 4, stn DW34, 24°55′ S, 168°22′ E, 515 m, 7 March 1989]; 1, NMNZ M.297232 [Smib 4, stn DW34].

Material Examined and Distribution: More than 60 lots, with several hundred live-taken specimens and empty shells, from the Norfolk Ridge, mainland New Caledonia off Ile des Pins, Grand Passage between mainland New Caledonia and Récifs d'Entrecasteaux, and banks on Lord Howe Ridge, alive at depths between 350 and 580 meters. Not found during research cruises to the Solomon Islands, Vanuatu, or Fiji.

Type Locality: South of New Caledonia: Norfolk Ridge, Kaimon Maru Bank, 24°45′ S, 168°06′ E, 600–896 m [Norfolk 2, stn DW 2091].

Remarks: Throughout their range, populations of *Bolma castelinae* are remarkably stable in shape and sculpture, and do not show geographical or bathymetrical variation. In Magalie Castelin's molecular tree (pers. comm.), *B. castelinae* is nearest to a possibly new species from the Solomon Islands tentatively identified by us as *B.* cf. *bartschii* (Dall, 1913). The latter has a peripheral cord with fewer, stronger spines, overhanging a broader, concave subsutural ramp; the spiral cords are broad, with narrow interspaces; and the basal disc is sculptured with beaded cords and bears a thin callus. Of the species present in New Caledonia, *B. castelinae* most resembles *B. recens* (Dell, 1967), but molecular analyses have confirmed that they are distinct. *B. castelinae* always has 3 rows of short scaly spines on the middle part of the last whorl: one on peripheral and basal angles and one between them, and a smooth and glossy base. In *B. recens*, the central row of spines is weak or absent, and flanked by numerous spiral grooves, and the basal disc is sculptured with concentric cords.

Etymology: The species is named after Dr (Ms) Magalie Castelin, whose molecular work has resulted in robust species delimitations in the genus *Bolma*.

Bolma pseudobathyraphis new species
(Figures 8–14)

Bolma guttata—Bouchet and Métivier, 1983: 10, figs. 4–6 [not figs. 7–8, which represent *B. fuscolineata* Alf and Kreipl, 2009].

Description: Shell large for genus, trochoid with very convex whorls, taller than wide, spire angle about 75°, rather thin shelled and light. Teleoconch of 7 to 7½ whorls, first 2 whorls planispiral, next 3 rather flat-sided, last two strongly convex with narrow, flat, subsutural ramp and overhanging peripheral cord, giving impression of a very deep, channelled suture. Periphery and basal cords weakly delimited, peripheral cord bearing row of short to very short, triangular, scaly spines which become evanescent near the peristome. Sculpture of fine, prosocline, axial lamellae extending on spire as well as on base, and strong, beaded spiral cords; on third whorl, single subsutural cord above periphery, number increasing to 4 on penultimate whorl, and to 7 on last whorl; space between peripheral and basal cords with three cords, central one stronger, bearing short scaly spines; base with 5 beaded cords. Columella smooth and evenly rounded, basal callus thick around columellar margin, thin on basal disc. Aperture oval, outer lip expanded, but not flaring, in adult specimens. No umbilicus. Background color light brown or light purple, occasionally more white or pink, distinctly darker above periphery, and with or without small, purple-brown spots between the beads on spire as well as on base. Columella white and nacreous, aperture nacreous within. Operculum thick and heavy, oval with convex, sometimes wrinkled, surface, white. Dimensions of holotype: Height 42 mm, diameter 37.5 mm, operculum largest diameter 17.1 mm.

Holotype: MNHN 22825 (lv).

Paratypes: 1, MNHN 22826, same locality as holotype; 1, ZRC.MOL.2955 [Smib 4, stn DW65, 22°55′ S, 167°15′ E, 400–420 m, 10 Mar. 1989]; 1, NMNZ M.297233 [Smib 2, stn DW6, 22°56′ S, 167°16′ E, 442–460 m, 17 Sep. 1986].

Material Examined and Distribution: *Bolma pseudobathyraphis* is the most abundant *Bolma* species in New Caledonia, with about 200 lots comprising ca. 1000 live-taken specimens and shells, from the Norfolk Ridge, mainland New Caledonia off Ile des Pins, Grand Passage between mainland New Caledonia and Récifs d'Entrecasteaux, banks on Lord Howe Ridge, and the

Loyalty Ridge, alive at depths between 240 and 530 meters. Not found during research cruises to the Solomon Islands, Vanuatu or Fiji.

Type Locality: Norfolk Ridge, south of New Caledonia, 23°42′ S, 168°16′ E, 377 m [Norfolk 2, stn CP2050, 24 Oct. 2003]

Remarks: *Bolma pseudobathyraphis* is very stable in shape, sculpture and size, except on Lord Howe Ridge where there exists a morph with long spines on the periphery (Figure 14), which however is not molecularly distinct.

Bouchet and Métivier (1983) had assigned their New Caledonia material to Bolma *guttata* (A. Adams, 1863), because of its superficial resemblance to the Indian Ocean populations described as *Bolma bathyraphis* (E.A. Smith, 1899), treated by Beu and Ponder (1979) as a subspecies of *B. guttata*. However, *B. pseudobathyraphis* differs from *B. bathyraphis* by its very convex whorls and deep suture, and a spiral sculpture of spiny, rather than rounded, beads. Juveniles of *B. pseudobathyraphis* also superficially resemble *B. fuscolineata* Alf and Kreipl, 2009, and had been confused with it by Bouchet and Métivier (1983), but they differ by their much higher last whorl and aperture, more widely spaced peripheral and basal cords, and more uniform color pattern (Figures 11–12 vs. 15–16).

In Magalie Castelin's molecular tree, *Bolma pseudobathyraphis* is nearest to to *B. millegranosa* (Kuroda and Habe, 1958) and to material from off Mozambique identified by us as *B. gilchristi* (Sowerby, 1903) [which may or may not be a synonym of *B. bathyraphis*]. *Bolma millegranosa* and *B. gilchristi* have smaller adult size, less convex whorls, and a peripheral cord situated very low on the whorl, bearing long deltoid spines on the periphery, albeit shorter in *gilchristi* than in *millegranosa*. *Bolma millegranosa* also differs by having a flaring outer lip in fully adult specimens.

Two other species which have not been sequenced resemble *Bolma pseudobathyraphis* because of their relatively high spire, namely *B. girgylla* (Reeve, 1843) and *B. kermadecensis* Beu and Ponder, 1979. *Bolma girgylla* is broadly distributed but rare in the Southwest Pacific (including New Caledonia); it differs by its flatter base, primary rows of wide, bilobed spines on the peripheral and basal cords, and the orange color of the columellar callus covering only part of the umbilical region. *Bolma kermadecensis*, only known from the dead and worn holotype from the Kermadec Islands, also has a flatter base, and has a dark pinky fawn color.

Etymology: From its superficial resemblance with *Bolma bathyraphis*, with which it had originally been identified.

Bolma kreipli new species
(Figures 17–20)

Description: Shell small for genus, trochoid, slightly taller than wide, spire angle 70°, thick and solid. Teleoconch of 5 ¾ whorls, first two whorls planispiral, third whorl with flat sides, last two whorls rather convex with low peripheral cord bearing strong, projecting spines (the spines were significantly chipped during shipping after the photos were taken), basal cord weakly delimiting convex base. Sculpture of indistinct, fine axial lamellae and beaded spiral cords, number of cords increasing from 4 on third whorl to 10 above periphery of last whorl, adapical cord stronger; interspace between periphery and basal cord with 3 beaded cords; base axially (radially) lamellate with 6 beaded cords, unevenly spaced with gap between the 2 cords that surround umbilical callus and rest of cords. Columella smooth and evenly rounded, bearing an indistinct tooth abapically, basal callus very thin, transparent, aperture oval, outer lip barely expanded. No umbilicus. Color and color pattern variable, background color creamy white, light brown or beige, with irregular purple, red or brown flames, base with purple dots irregularly placed between beads. Columella white, aperture nacreous within. Operculum thick and heavy, oval with a convex, wrinkled surface and small, flat marginal edge, white. Dimensions of holotype: height 14.2 mm, diameter 13.5 mm. Operculum diameter 4.9 mm.

Holotype: MNHN 22827 (lv).

Paratype: 1 (lv), MNHN 22828, from 22°32'S, 167°32′E, 155 m, 9 Sept. 1989 [Smib 5, stn DW82].

Other Material Examined: Musorstom 4: stn DW203, 22°36′ S, 167°05′ E, 105–110 m, 27 Sept. 1985, 2 dd. Lagon: stn 316, 22°35.3′S, 166°54.0′ E, 68 m, Nov. 1984, 1 lv; stn 386, 22°37′ S, 167°09′ E, 128 m, Nov. 1984, 1 dd; stn 397, 22°39′ S, 167°11′ E, 125 m, Nov. 1984, 1 lv.

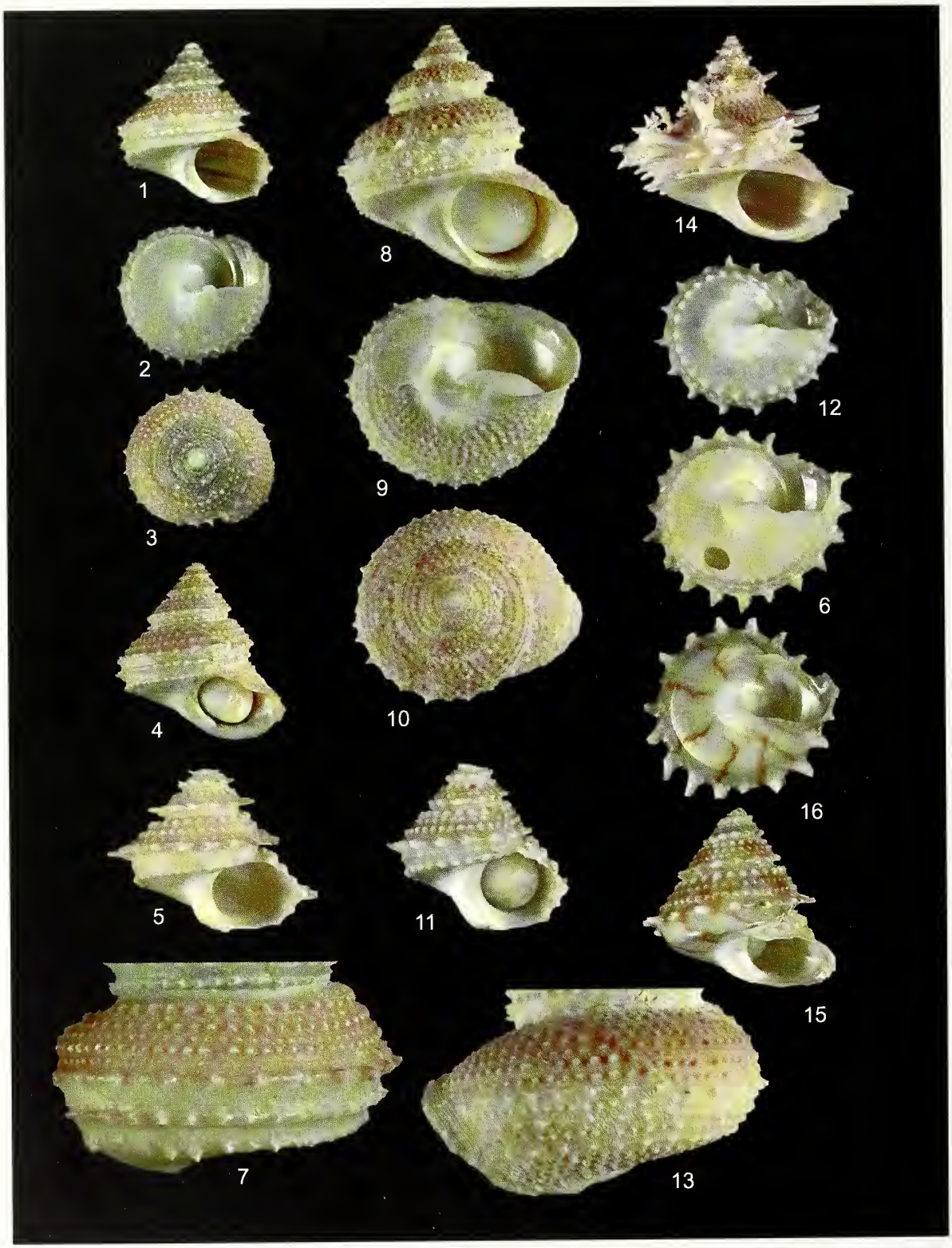
Type Locality: Between New Caledonia and Ile des Pins, 22°34′ S, 167°10′ E, 75 m [Musorstom 4, stn DW231, 1 Oct. 1985].

Discussion: We have had no molecular material of *Bolma kreipli*, and our comparisons are entirely based on phenotypic resemblance. *Bolma kreipli* resembles *B. persica* (Dall, 1907) but differs from it by its overall higher shape, more convex whorls and base, less angular periphery and basal angle, distinct periumbilical cords, and non-nacreous columella. At 22 mm, *Bolma persica* also reaches a larger adult size than *B. kreipli*.

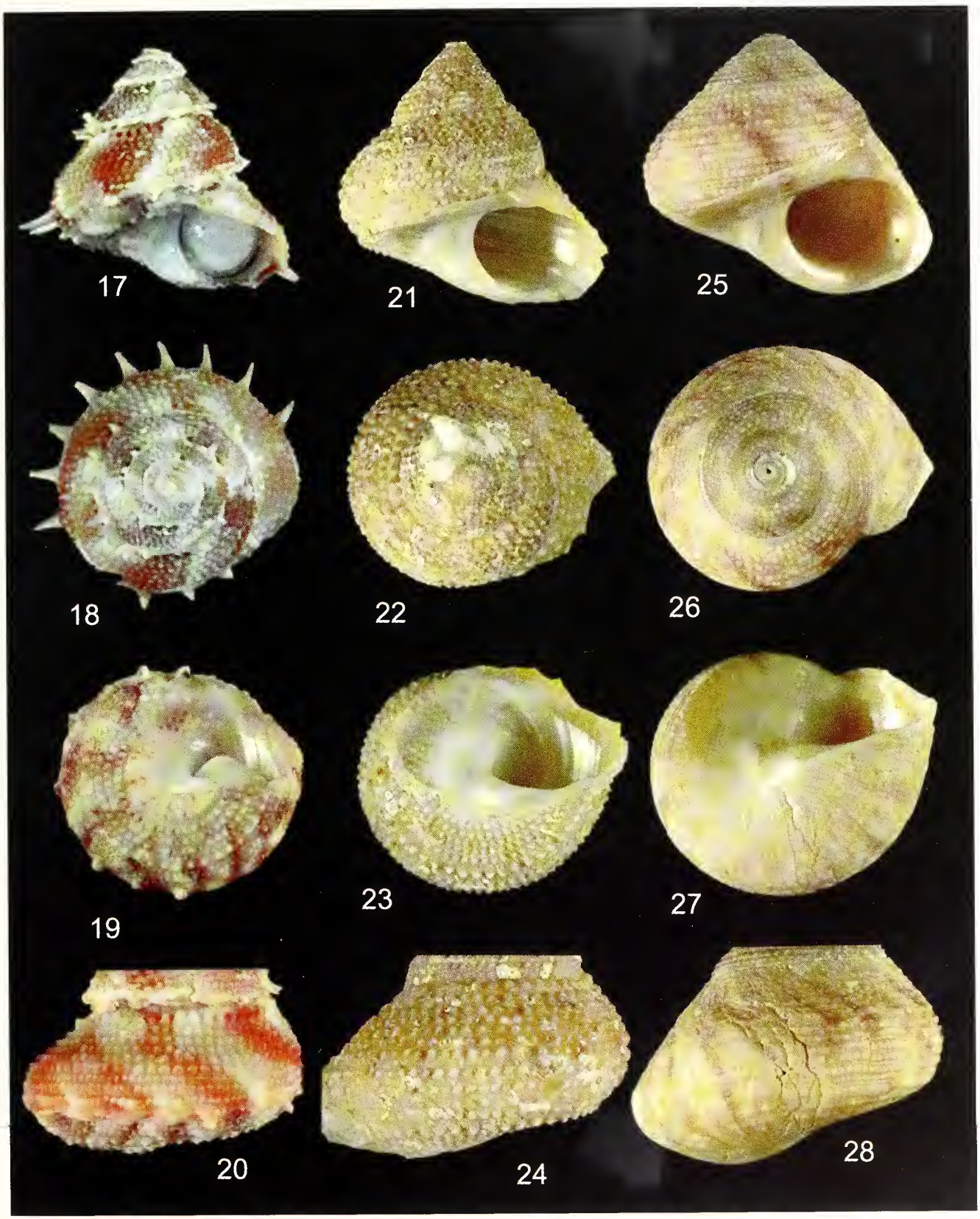
Etymology: After Kurt Kreipl, an authority on *Bolma* and other turbinids.

Bolma mainbaza new species
(Figures 21–24)

Description: Shell medium-sized for genus, trochoid, as tall as wide, spire angle about 75°, rather thin shelled. Teleoconch of 6 whorls, first 2 whorls planispiral, next whorls regularly convex, separated by narrow, deep suture; on spire whorls, peripheral cord covered by successive whorl, on last whorl not demarcated and resembling any of the spiral cords; basal cord distinctly



Figures 1–16. *Bolma* species from New Caledonia. **1–7.** *Bolma castelinae* new species. **1–3.** Holotype, MNHN 22823, height 25.2 mm. **4.** Paratype, MNHN 22840, adult with fully developed outer lip, 18°54′ S, 163°24′ E, 352–397 m [Halical 1, stn DW02], height 27.5 mm. **5–6.** Juvenile, 24°56′ S, 168°22′ E, 520 m [Smib 3, stn DW01], height 9.7 mm. **7.** Holotype, detail of last whorl. **8–14.** *Bolma pseudobathyraphis* new species. **8–10.** Holotype, MNHN 22825, height 42 mm. **11–12.** Juvenile, 18°56S, 163°24′E, 380–400 m, Halical 1, stn DW01], height 8.5 mm. **13.** Holotype, detail of last whorl. **14.** Specimen with unusually spinose sculpture, 24°45′ S, 159°43′ E, 328–463 m [Ebisco, stn CP2505], height 34.6 mm. **15–16.** *Bolma fuscolineata* Alf and Kreipl, 2009, 22°56′ S, 167°15′ E, 427–433 m [Norfolk 1, stn DW1733], height 8.6 mm.



Figures 17–28. *Bolma* species. **17–20.** *Bolma kreipli* new species, holotype, MNHN 22827, height 14.2 mm. **21–24.** *Bolma mainbaza* new species, holotype, MNHN 22829, height 21.2 mm. **25–28.** *Bolma tantalea* new species, holotype, MNHN 22831, height 23.4 mm.

stronger, delimiting poorly defined basal disc. Sculpture of fine prosocline lamellae and beaded spiral cords, number above peripheral cord increasing from 2 on third whorl, to 6 on penultimate whorl and 9 on last whorl, adapical cord stronger; peripheral cord bearing spines on spire whorls, simply beaded on last whorl; interspace between peripheral and basal cords bearing one beaded cord. Base moderately convex, sculptured by 5 beaded cords, unevenly spaced, with gap to basal cord. Columella smooth and evenly rounded, with thin, polished basal callus extending over the base. No umbilicus. Outer lip expanded in adult specimens. Background color light pinkish brown to fawn, beads usually lighter, white to brown, not forming any pattern. Columella porcellaneous white. Operculum ovate, outer side white, regularly convex, weakly pustulose at center. Dimensions of holotype: Height 21.4 mm, diameter 20.4 mm, operculum largest diameter 8.6 mm. Largest specimen reaching a size of about 24 mm.

Holotype: MNHN 22829 (lv).

Type locality: Mozambique Channel, off southern Mozambique, Almirante Leite Bank, 26°12′ S, 35°02′ E, 228–230 m [MAINBAZA, stn DW3167, 16 April 2009].

Paratypes: 14: MNHN 22830, 11 (6 lv, 5 dd); Natal Museum L7886/T2579, 1 (lv); Museu de Historia Natural de Maputo, Mozambique, 1 (dd); Coll. J. Rosado, Maputo, 1 (lv); all from the type locality.

Remarks: Magalie Castelin has obtained DNA from the tissues of this new species, but sequencing has, at the time of writing, been unsuccessful. Our comparison with other species is thus purely phenotypical. Of the six species of *Bolma* recorded until now from the southwestern Indian Ocean, *Bolma mainbaza* resembles *B. flava* Beu and Ponder, 1979 [a full species, or a geographical subspecies of *B. tamikoana* (Shikama, 1973), as treated by Beu and Ponder] but the latter differs by having more depressed whorls, a distinct, spine-bearing peripheral cord, more numerous and finer spiral cords (10 above periphery of last whorl, 3 between peripheral and basal cords, 16 on base), and a color pattern consisting of brownish to purplish flames on a yellowish background; *B. mainbaza* lacks spines and is fawn-colored with irregularly scattered, small, well defined brown spots.

Etymology: Named after the cruise Mainbaza, an acronym for *MA*puto, *IN*hambane, *BA*zaruto and *ZA*mbeze, Mozambique localities off of which deep-water transects were carried out.

Bolma tantalea new species
(Figures 25–28)

Description: Shell of average size for the genus, trochoid, slightly broader than tall (h/d = 0.95), spire angle about 85°, shell thick and solid. Teleoconch of about 5.5 whorls, suture shallow, adapical whorls almost flat, last whorl moderately convex, periphery and basal disc poorly demarcated. First 2.5 teleoconconch whorls smooth between subsutural, strongly beaded cord and peripheral cord bearing blunt spines, 14 per whorl, covered by successive whorl. Subadult and adult whorls with narrow smooth ramp adapically of subsutural cord, additional spiral beaded cords occupying space between subsutural and spineless, peripheral cord; 4 cords on 3rd whorl, 5 on exposed part of penultimate whorl, 7 plus a couple of secondary ones above periphery of on last whorl; 2 primary and 2 secondary cords between periphery and basal angle, beads on periphery and basal cord coalescent. Base slightly convex, sculptured with 2 weakly beaded and ca. 12 smooth spiral cords that become obsolete toward columellar region. Columella smooth and evenly rounded, umbilicus closed by thick, slightly yellowish white polished callus, covering about 1/3 of the basal disc. Outer lip hardly reflected at all. Background color pinkish ivory, with darker, brownish-purple axial veins. Columella and aperture nacreous. Operculum rounded, outer side white, nucleus very slightly depressed, greenish brown. Dimension of holotype: Height 23.4mm, diameter 26.3mm, operculum largest diameter 10.0 mm.

Holotype: MNHN 22831 (lv).

Paratype: MNHN 22832, 1 (dd) from off Raiatea, Society Islands, 16°53′ S, 151°21′ W, 440–490 m, 18 Oct. 2009 [TARASOC, stn DW3451].

Material Examined and Distribution: Only known from the type material and several fragments from the western part of the Tuamotus chain attributed to the species.

Type Locality: French Polynesia, Society Islands, Tahiti, 17°48′ S, 149°22′ W, 390–790 m [TARASOC, stn DW3488, 23 Oct. 2009].

Remarks: *Bolma tantalea* is very distinctive among South Pacific Bolmas by its very compact overall appearance. It vaguely resembles *B. recens* which differs by a pointed spire, deep and often even canaliculate suture, well marked peripheral and basal angles separated by an almost flat interspace, a spiral sculpture with fewer (usually up to 5 above periphery) beaded cords and short triangular spines on the periphery, at least on spire whorls. Spineless forms of *Bolma tamikoana* can be separated by their orange columellar callus. *Bolma opaoana* has a pointed spire and its color is fawn with brownish flames, and a slight orange blotch on the columella and columellar callus. *Bolma midwayensis* Habe and Kosuge, 1970, has a pointed spire and deep suture, and its color is whitish with pink clouds.

Etymology: *Tantaleus, -a, -um*, is an adjective formed after Tantalus, the mythological character symbolic of torment. During the TARASOC cruise only tantalizing shell fragments were first sampled, then during the third week a broken adult was taken, and the live-taken holotype was finally obtained after more than 120 dredge hauls, just three days before the end of the cruise.

ACKNOWLEDGMENTS

The New Caledonia material originates from many cruises listed by Bouchet et al. (2008), and we are especially grateful to our colleagues Marie-Catherine Boisselier, Magalie Castelin, Pierre Lozouet, Bertrand Richer de Forges, and Sarah Samadi for companionship at sea and unpublished molecular results in the laboratory. The specimens from off Mozambique were collected by R.V. Vizconde de Eza during the MAINBAZA cruise in April 2009. The cruise was operated by Muséum National d'Histoire Naturelle (MNHN) and Instituto Español de Oceanografia (IOE), as part of a cluster of Mozambique-Madagascar expeditions funded by the Total Foundation, Prince Albert II of Monaco Foundation, and Stavros Niarchos Foundation, and conducted by MNHN and Pro-Natura International (PNI). Philippe Bouchet is grateful to Ana Ramos and Eduardo Balguerias for making this cruise possible. Like many other expeditions in the Tropical Deep-Sea Benthos program, the Tarasoc cruise took place on board IRD's (Institut de Recherche pour le Développement) R.V. Alis, and its success owes much to the skills of its officers, Raymond Proner, Jean-François Barazer and Loïc Le Goff. Finally, we are grateful to Magalie Castelin for having made her molecular results available to us to facilitate species-level comparisons of the new species described in this paper.

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The use of aquatic plants by populations of the zebra mussel (*Dreissena polymorpha*) (Bivalvia: Dreissenidae) in a small glacial lake

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ABSTRACT

We examined the early life history of the zebra mussel (*Dreissena polymorpha*) in a small Pennsylvania lake with limited natural hard substrate. Veligers first appear in May, and settled on *Nuphar* (Yellow Water Lily) stems and concrete substrates in equal densities. Later cohorts, however, did not settle on the stems. Juveniles on stems abruptly abandoned their attachment in late August as the plant tissue began senescence. Aquarium experiments demonstrated that juveniles retained the ability to seek and find alternate substrates even after several months. Year-old zebra mussels were markedly unsuccessful in comparison. We speculate that in lakes with limited natural hard substrates aquatic plants may play an important role in zebra mussel recruitment, although juveniles must be able to locate alternate substrates as plant populations senesce at the end of the season. The resulting high mortality may limit mussel populations in these lakes.

Additional keywords: Invasions, substrate, life history, aquatic macrophytes

INTRODUCTION

Following the introduction of the zebra mussel (*Dreissena polymorpha*) to Lake St. Clair in the 1980s, much attention has been focused on the rapid dispersal and the environmental requirements of this invader (Griffiths et al. 1991, Strayer 1991, Hincks and Mackie 1997). Ludyanskiy et al. (1993) predicted that by the year 2000 the zebra mussel would inhabit all of North America's rivers, lakes, and reservoirs that fit within its broad range of ecological requirements. However, due to the limitations of overland dispersal the invasion of small inland lakes disconnected from navigable waters is taking much longer than initially anticipated (Kraft and Johnson 2000, Bossenbroek et al. 2001). The glaciated portion of northwestern Pennsylvania, for example, has eight natural lakes all between 18 and 74 km from the south shore of Lake Erie, the most immediate source of veligers and adults, and all meeting the ecological requirements of *D. polymorpha*. To date, however, only two of them have established populations of *D. polymorpha* (Butkas and Ostrofsky, 2006) in spite of considerable recreational boat traffic among these inland lakes, and between these lakes and Lake Erie where *D. polymorpha* was first observed in 1989 (Griffiths et al. 1991). Observations from other inland lake districts in Illinois, Indiana, Michigan, New York, and Wisconsin have reported similarly slow dispersal and colonization (Miller and Haynes 1997, Kraft and Johnson 2000, Johnson et al. 2001). Consequently, the bulk of the published North American work on *D. polymorpha* has been from the Great Lakes and major river systems. The effects of this invader on small, inland lake ecosystems have received far less attention.

One of the characteristics of lakes in northwestern Pennsylvania and lakes in similar geographical settings is the relative paucity of natural hard substrates. These lakes tend to be small, with limited wind-generated wave energy to move fine sediments offshore. This combination of characters results in lakes with soft, muddy or peaty sediments right up to a shoreline that transitions through a zone of floating-leaved and emergent aquatic vascular plants. Rock outcrops and gravel bars are exceptionally rare. With the exception of the shells of native unionid mussels, the hard substrates that do exist are invariably man-made: docks, pilings, retaining walls, boat hulls, and waterlogged pieces of wood and other debris. Several studies have suggested that the colonization success and ultimate carrying capacity of *D. polymorpha* populations is determined by the availability of suitable hard substrates for attachment rather than by the quality and quantity of filterable food resources (Brady et al. 1995, Grigorovich and Babko 1997, Lewandowski 2001, Burlakova et al. 2006). There have been several studies that investigate the relative preferences displayed for

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substrate type, orientation, and texture by settling *D. polymorpha* veligers (Marsden and Lansky 2000, Kobak 2004, Czarnoleski, et al. 2004) but one possible substrate that has not received much attention is the surface of aquatic vascular plants (Lewandowski 2001). *Dreissena polymorpha* is known to attach to aquatic vascular plants (Horvath and Lamberti 1997, Diggins et al. 2004, Muskó and Bakó 2005). Hence, vascular plants may play an important role in the establishment and persistence of invasive populations in lakes with limited alternate hard substrates. However, while aquatic vascular plants offer considerable surface area, and often grow in dense stands that confer attached mussels some protection from predation by fish, they are seasonal and lack long term stability (Grigorovich and Babko 1997, Ozimek 1997). Most species rapidly senesce with the onset of cooler weather and shorter day lengths. To survive, attached biota must have the ability to abandon senescent plants and seek another, more permanent substrate.

In order to fully understand the ecology of the zebra mussel and the impacts it will cause as it continues to spread throughout North America, it is essential that we understand species interactions within small-lake ecosystems. In this study, we examined the early life history of a zebra mussel population in a small inland lake in Pennsylvania. We were particularly interested in the potential role of aquatic vegetation in a lake that otherwise provides few hard substrates. We sought to determine if aquatic plants could provide a substrate that was as acceptable to settling *D. polymorpha* veligers as more traditional hard substrates, and if, at the end of the vegetative growing season, settled juveniles retained the capacity to seek alternate substrates as the plant tissue senesced.

MATERIALS AND METHODS

All fieldwork was conducted in Sandy Lake, a small (~ 60 ha), moderately hard (total alkalinity ~ 70 mg/L) kettle lake located in Mercer County, Pennsylvania (41° 20.71' N, 80°06.43' W). Sandy Lake has a drainage basin area of only 7.2 km^2 consisting mostly of forest (52.6%) and low intensity agriculture (pasture/hay 39.7%, row crops 3.6%; USGS, 2000). Although no bathymetric map has been made to date, the maximum noted depth was 12 m. The lake stratifies from May through mid-October, with the thermocline at approximately 5 m. Hypolimnetic water below 9 m became anoxic by early July. Springtime total phosphorus concentration (~ 13 ug/L) and summer average Secchi disk visibility (3.5 m) suggest that the lake is oligo-mesotrophic (Ostrofsky, unpubl.). Sandy Lake is used primarily for fishing, swimming, and waterskiing. *Dreissena polymorpha* were first observed in the lake in 2000 (J. Widel, Lakeside Park Co., personal communication) and have been a conspicuous feature on hard surfaces ever since.

Water samples for the enumeration of planktonic veligers were collected weekly from three mid-lake locations from mid-May to late-October 2004 (Figure 1). Two liters of epilimnetic water from each location were filtered through 0.45 µm membrane filters. Filters were dried, cleared with immersion oil, and mounted on slides. Veligers were identified using cross-polarized microscopy (Johnson 1995). Lengths of 200 (or n, if n< 200) veligers were measured to the nearest 10 µm using an ocular micrometer.

We monitored settlement of juvenile *D. polymorpha* on both artificial substrates and aquatic vascular plant surfaces. We used 0.093 m^2 concrete tiles (12"×12") placed in three lake locations (Figure 1) at a depth of approximately 1.5 meters. Tiles were put in the lake in May and retrieved in late August/September after veligers had disappeared from the water column. Juveniles found were preserved in 70% ethanol. The length of each juvenile was measured to the nearest 0.1 mm using a dissecting microscope and an ocular micrometer. We monitored the settlement of juvenile *D. polymorpha* on the submersed stems of the Yellow Water Lily *Nuphar variegata*. We collected ten individual stems (~0.75 m in length) from each of five macrophyte beds around the lake at weekly intervals from mid-May through September. Each stem was scraped to remove all attached organisms. All scrapings were preserved in 70% ethanol until examined. The total number of juveniles found on each stem was recorded. For each date sampled 200 (or n, if n< 200) juveniles were randomly selected and measured to the nearest 0.1 mm. Both veligers and settled juveniles were grouped into size classes and size-frequency graphs were constructed to estimate spawning and settling cohorts across the growing season.

To determine the ability of *D. polymorpha* to migrate to alternate substrates we suspended lake-collected macrophyte stems with 100 attached juvenile mussels in coarse mesh netting at the surface of each of 3 replicate 37 L (10 gal.) aquaria in the lab. The bottom of each aquarium was covered with a patchwork of unglazed ceramic tiles (15×15 cm) and fine lake sediments in a 1:1 substrate/sediment ratio. Each tank was filled with aerated lake water. After two weeks the macrophyte

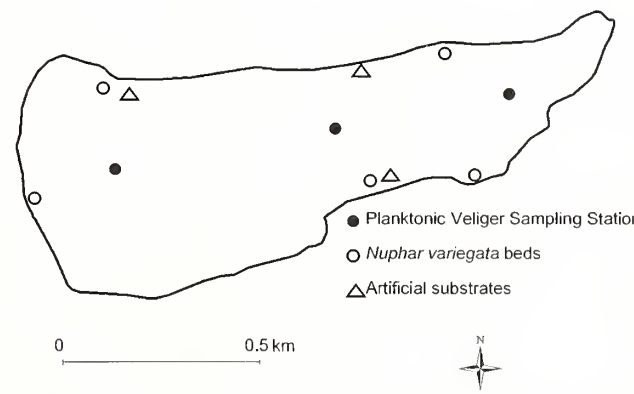

Figure 1. Map of Sandy Lake, Pennsylvania showing sampling locations for *Dreissena polymorpha* veligers, *Nuphar* beds, and artificial substrates.

stems had senesced, and stems, tiles, and sediments were examined for juveniles. We used χ^2 to test the null hypothesis of random settling (frequencies on tiles = frequencies on soft sediment).

To examine differences in the ability to seek and find new substrate as a function of mussel age, we established 8 replicate 37 L aquaria in the lab, each with fine lake sediment, aerated lake water, and a single tile giving a 1:5 tile to soft sediment ratio. To each aquarium we introduced 5 juvenile (6–11mm) and 5 adult (20–30 mm) *D. polymorpha* individuals to the soft sediment. Very few lake-collected mussels were found between 11 and 20 mm suggesting that these two size classes were from different spawning seasons. Tiles were examined daily and the number of juveniles and adults censused for 1 week. The rates at which juvenile vs. adult mussels accumulated on the tiles was taken as a measure of their ability to find alternate substrates.

RESULTS

Veligers were first observed in the plankton in late May when the epilimnetic water temperature was 21°C. There were no significant differences ($p > 0.05$, ANOVA) in veliger densities among the three lake sampling sites so data from all sites were pooled. Veliger density increased rapidly to a maximum of 17,500/m^3 (± 5,635 s.e.) in late June, then rapidly decreased, disappearing from the plankton by early August (Figure 2). Measured veligers varied in length from 60 to 250 µm, and size-frequency analysis (Figure 3) and changes in density suggest the presence of three cohorts: large ones in late May and late June, and a very much smaller one in late July.

Settled larvae first appeared on *Nuphar* stems in late June (Figure 4), reaching maximum densities in mid-July of 62 (±20.7 s.e.) individuals per stem (approximately 1 individual/cm^2). Settled juveniles showed a strong tendency to aggregate on a few stems rather than to accumulate evenly among all available stems. In 50% of the site x date collections the variance:mean ratio of settled juveniles on stems was significantly greater than one (χ^2-test). The smallest measured juveniles were 200 µm, approximately the same as the maximum veliger size in

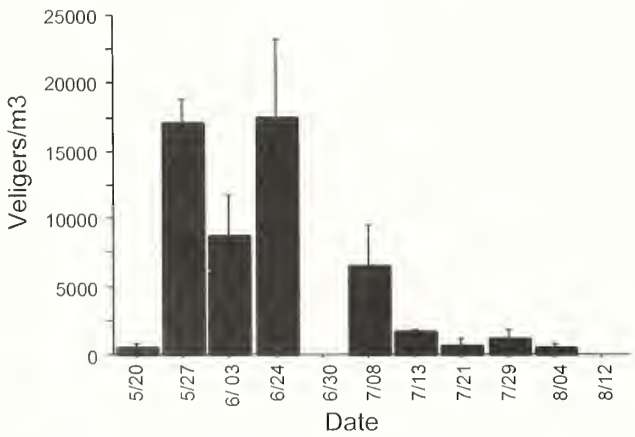

Figure 2. Mean *Dreissena polymorpha* veliger densities (± 1 std. error) in the epilimnion of Sandy Lake.

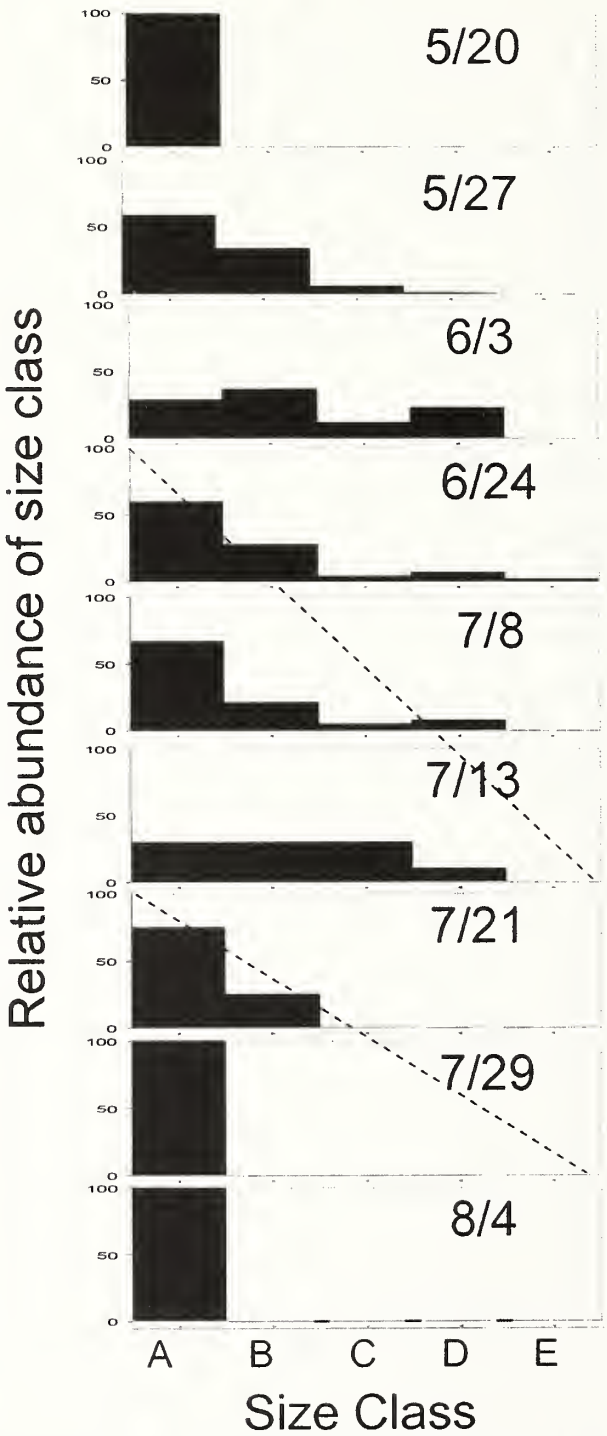

Figure 3. Size-frequency distribution of Sandy Lake *Dreissena polymorpha* veligers. Lines separate different cohorts suggested by both density and size distribution data. Size class A = <110 µ, B = 111–150 µ, C = 151–190 µ, D = 191–230 µ, E = >231 µ.

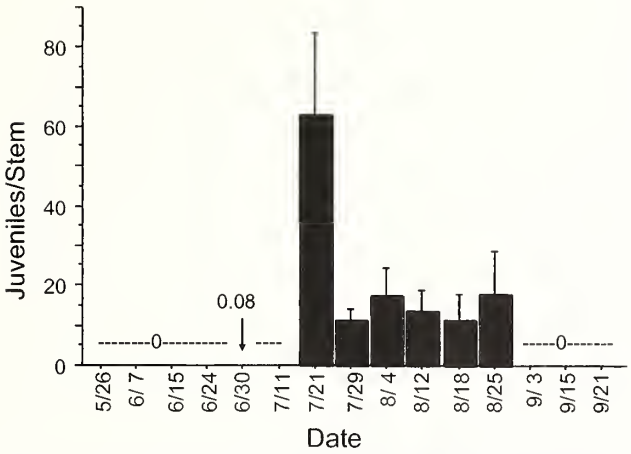

Figure 4. Mean density of juvenile *Dreissena polymorpha* (± 1 std. error) on stems of *Nuphar variegata* in Sandy Lake.

the plankton. Visual analysis of size-frequency data of the settled juveniles on stems (Figure 5) suggested only a single cohort with high initial mortality (77%) but very little mortality after late July. Juveniles abruptly disappeared from stems after late August. Adult *D. polymorpha* between 6 and 17 mm in length were occasionally observed attached to *Nuphar* stems, particularly early in the season. Individuals of this size were undoubtedly from the previous growing season. Concrete tiles collected at the end of the summer had densities of settled juveniles ranging from 0.11 to 2.69 individuals per cm^2 (mean =1.0, s.e. = 0.9). There was no significant difference between the density of settled juveniles on concrete tiles and the maximum density measured on *Nuphar* stems ($p > 0.05$, t-test).

In the laboratory experiments approximately half (46%) of the juveniles on suspended vascular plant stems in the aquaria abandoned their attachment sites within two weeks as the stem senesced (Table 1). We anticipated equal numbers would be recovered from the tiles and from soft sediments if displaced juveniles were incapable of migrating to firm substrates. We found that all of the displaced juveniles were recovered either on the tiles (26.7±7.7 s.e.) or attached to the aquarium walls (19.0±5.1 s.e.). None was recovered from the soft sediment. Those that remained attached to the plant material were assumed to be dead.

In the migration experiment comparing juveniles and adults, juveniles were found on the tile early and their numbers steadily increased (Figure 6). Adults appeared on the tiles late and in very small numbers. Rates of arrival on the hard substrate were 3.54 and 0.29 individuals/day for juveniles and adults, respectively. These rates were significantly different ($p < 0.05$, t-test for slopes).

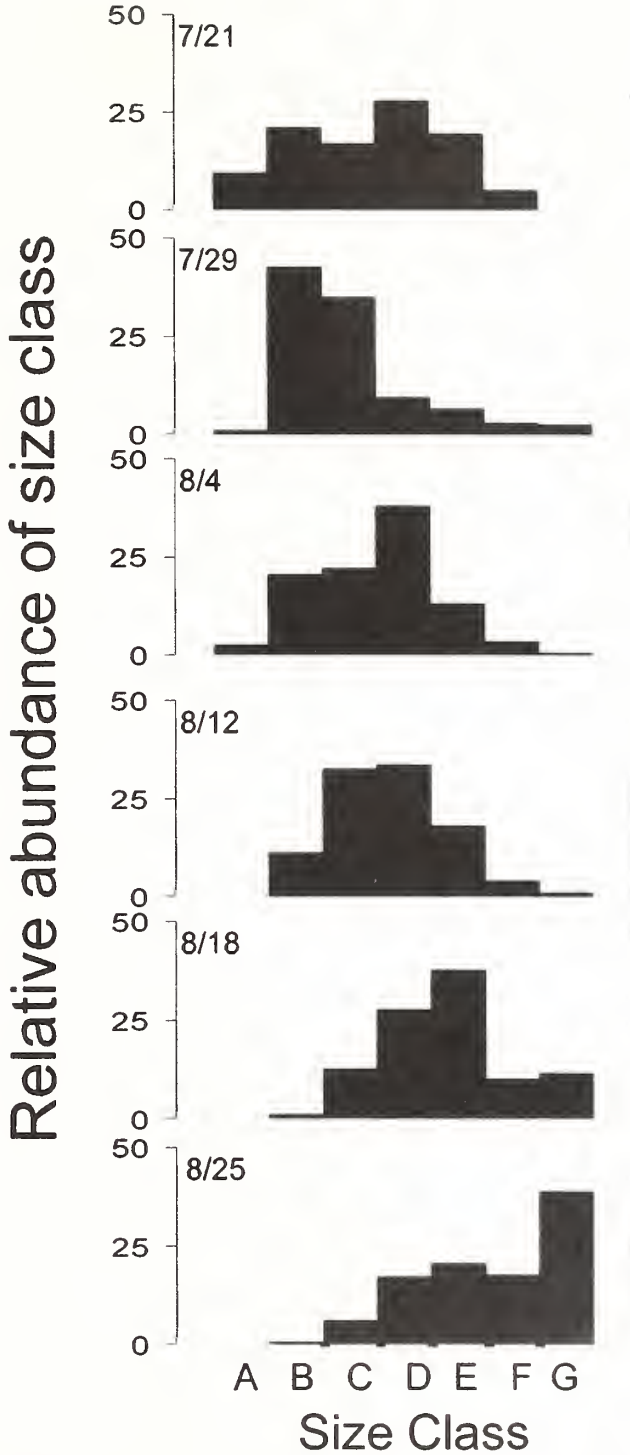

Figure 5. Size-frequency distribution of juveniles on *Nuphar variegata* stems. Data suggest a single cohort. Size class A = <400 µ, B = 401–900 µ, C = 901–1400 µ, D = 1401–1900 µ, E = 1901–2400 µ, F = 2401–2900 µ, G = >2901 µ.

DISCUSSION

An overview of the life history of *Dreissena polymorpha* given by Ludyanskiy et al. (1993) based largely on the European literature suggests that initial veliger size is about 70 µm and that these veligers increase rapidly in size (up to 300 µm) in 5 days to 5 weeks, at which time they can no longer remain suspended in the plankton and

Table 1. Distribution of juvenile mussels initially attached to senescing aquatic plants after two weeks. Approximately 46% of the mussels left the plants and successfully located an alternate hard substrate for reattachment. No mussels were found in the soft sediment.

	Tank 1	Tank 2	Tank 3
Initial # Mussels on Plants	100	100	100
No. Mussels on Tile	12	30	38
No. Mussels on Aquarium Wall	22	26	9
No. Mussels in Soft Sediment	0	0	0
Total Migrating	34	56	47
Remaining on Plants/Dead	66	44	53

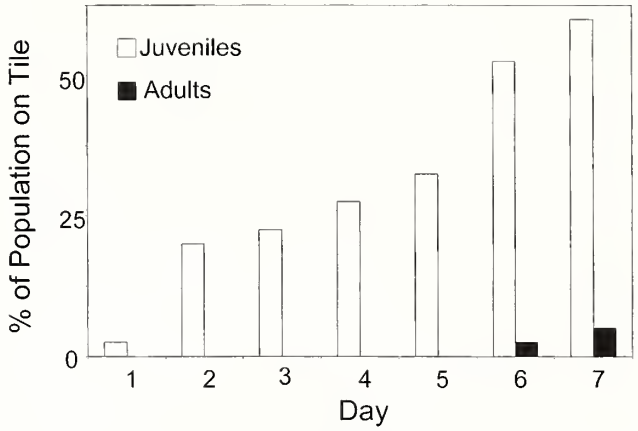

Figure 6. Migration of juvenile and adult *Dreissena polymorpha* from soft sediment to hard tile substrate in aquarium experiment.

settle on hard substrates. Veligers first appeared in Sandy Lake on May 20, and rapidly increased to a maximum density of about 17,500/m^3. The smallest veligers were 60 µm, and the largest were 250 µm. We tentatively identified three cohorts based on size-frequency analysis.

The first juveniles appeared on *Nuphar* stems on June 30, and by July 21 had reached a mean density of 62 individuals/stem (approximately 1 individual/cm^2). Size-frequency analysis of settled juveniles suggested only a single cohort (in contrast to possibly three veliger cohorts). Similarly, Wainman et al. (1996) found only a single three-week recruitment (settling) period in Lake Erie, also in July. We are confident that the first veliger cohort was the source of the settled juveniles because the smallest settled juveniles were approximately the same size as the largest of the veligers, and they overlapped temporally. The single cohort that successfully settled on *Nuphar* stems appeared to suffer high initial mortality, falling from a density of 62 individuals/stem to 11/stem in the first week. There was no further significant decrease in density until September 3, when densities fell to zero.

The abrupt loss of juveniles from plant stems at the end of August could be a consequence of increased predation—those on plant stems perhaps being particularly vulnerable/visible/available—or could be the result of a mass abandonment of these attachment sites as a consequence of some perceived change in substrate quality. In late summer, *Nuphar* stems become heavily coated with epiphytic microorganisms, and the stems lose their firmness – either condition might signal a deterioration of substrate quality to the mussels. That *Nuphar* stems are attractive settlement sites early in the summer is supported by our observation that mean juvenile density on stems is no different from mean density on concrete artificial substrates collected at the end of the summer although the aggregated distribution on plant stems, and the data from the literature on other hard surfaces suggest that they are attracted by slight differences among otherwise similar surfaces or to each other (Wainman, et al. 1996). The lack of any evidence for the settlement of the second and third veliger cohorts on stems as the season progresses suggests that these sites become less attractive.

The fate of juveniles that abandon their attachment to *Nuphar* stems is unknown. Newly settled juveniles have the ability to seek alternate attachment sites by crawling or by using byssal threads to resuspend themselves in the water column and resettle elsewhere (Griffiths, et al. 1991, Marsden and Lansky 2000), and Martel (1993) has documented juveniles up to 2 mm in length in the plankton of Lake Erie under conditions of high waves and strong currents. Lewandowski (1982) has noted the presence of plant remains in the byssus of 1 and 2 year old individuals found in benthic colonies. We are aware of no studies that have directly observed the fate of established juveniles that have abandoned their attachment sites after several weeks, however. Juveniles leaving attachment sites at the end of the summer in Sandy Lake were large enough (77% were greater than 2 mm in length) that resuspension is an unlikely option. Juveniles may simply fall to the sediment surface and crawl seeking a better substrate.

The aquarium experiments did show that these large juveniles were capable of locating and successfully attaching to hard substrates after leaving senescing plant material. All of those that abandoned the plant stems in aquaria were found either on the tiles or on the aquarium walls. None was found on the soft sediments. This ability to find alternate substrates is lost with time, and year-old individuals were markedly unsuccessful compared to the younger cohort. At Sandy Lake we frequently encountered relatively large (6–17 mm) *D. polymorpha* individuals attached to plant stems or to the undersides of *Nuphar* leaves, particularly early in the season. We speculate that these individuals represent the previous year's cohort that abandoned plant stems, failed to find an alternate substrate, persisted on the surface of the plant litter in the littoral zone over the winter, then had a serendipitous encounter with an emerging *Nuphar* shoot the following spring. Lewandowski (1982) has also noted that 99.5% of the individuals found on plants are less than 0.5 mm in length, indicating that they belong to the youngest cohorts.

In Sandy Lake, and in other inland lakes with limited natural hard substrates it is likely that a significant portion of the annual *D. polymorpha* settlement occurs on plant surfaces – not only the relatively firm stems of *Nuphar* and emergent vegetation, but on the softer foliage of submersed plants as well. The available surface area provided by plants vastly exeeeds that of alternate attachment sites. While the density of juvenile mussels on plants may be eomparable to that on other substrates, mortality is eonsiderably higher as a result of the need to abandon the plant surfaces with plant senescenee, and the low probability of encountering an alternate site even though juveniles retain the ability to seek these sites. The resulting high mortality may be sufficient to limit the size of the adult population in lakes with limited hard substrate.

Why have zebra mussels failed to eolonize small inland lakes in the midwestern US as anticipated by Ludyanskiy et al. (1993)? Johnson et al. (2001), noting low colonization sueeess in spite of dispersal events estimated in the hundreds or thousands, cite three possible reasons for this failure. First overland transport is inefficient and many mussels attaehed to boats or to aquatic plants entangled in boats and trailers, or earried in bait wells or in bilge water fall off or die before reaching a new colonization site. Second, boaters do not visit lakes randomly, but rather visit a small subset of the most popular ones and long-distance dispersal fits a gravity model rather than a diffusion model (Bossenbroek, et al. 2001). Finally, overland transport and inoculation of new sites may oeeasionally be suecessful, but the eolonists fail to found new populations. The causes of this failure are certainly varied. Butkas and Ostrofsky (2006) reported evidence of a failed introduction in Canadohta Lake likely due to too small an inoculum. Other introductions may fail as a result of inhospitable ehemical or physical characteristics of the new site, including a paueity of favorable substrates for attachment. Lewandowski (2001) has estimated the survival of settling veligers to be usually less than 1%, and even in lakes with unusually well developed littoral zones less than 5% simply by failing to find an appropriate substrate. Further, those that do find substrates may not survive winter freezing or ice scour (Brady et al. 1995) if those substrates are in shallow water.

Our data suggest that the earliest cohort of settling veligers in Sandy Lake do not diseriminate among substrates in that there was no significant difference between the density of juveniles on artifieial hard substrates (concrete tiles) and their density on *Nuphar* stems. Karatayev et al. (1998) observed similar results in a number of European lakes when eomparing juvenile mussel densities on a number of natural substrates ineluding aquatie plants. Later cohorts in Sandy Lake did not settle on the stems, or settled on them in very much redueed numbers, evidently finding them less suitable than did the earlier eohort. Nevertheless, the surfaee area of plant tissue available for settlement greatly exceeds the area of other substrates (Brady et al. 1995, Ozimek 1997), and Lewandowski (1982) estimated that more than 85% of the mussel population in 26 Masurian (Poland) lakes were using aquatie plants as substrates. However, the growing season of aquatic plants is shorter than the life of mussels, and on senescence mussels must abandon plant surfaees and seek alternate substrates if they are to survive. In Sandy Lake the density of juveniles on plants deelined abruptly at the end of August. Lewandowski (2001) similarly found that populations of first year mussels on plants decreased by 78% between August and September in Lake Czos due to plant senescence. Larger declines were seen in older mussels. Our laboratory experiments illustrate that these first year displaeed mussels have the ability to migrate in seareh of alternate substrates, and our finding larger, seeond year old mussels oeeasionally on plant surfaces indicates that at least some are successful in that search. Lewandowski (1983) reported similar findings—that 2 to 3 year old mussels were found on plant surfaees in low numbers, 99.8% of the individuals were juveniles that had settled that year. However the eumulative effect of low settlement suceess and low survival of those settling on aquatie plants must severely limit the populations of zebra mussels in lakes lacking more permanent hard substrates.

ACKNOWLEDGMENTS

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Description of *Calliotropis ceciliae* new species (Gastropoda: Chilodontidae: Calliotropinae) from off Chile

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ABSTRACT

A new species of *Calliotropis* is described from the vicinities of the Concepción Methane Seep Area (~36°S) and from additional material from off Antofagasta (northern Chile, ~22°S). It is compared to *C. pelseneeri pelseneeri* Cernohorsky, 1977, and *C. pelseneeri rossiana* Dell, 1990, from the adjacent Antarctic area, which differ notably from the new species by having a thicker supra-peripheral spiral cord, more angulate whorls, and a more lamellose sculpture present in the subspecies *pelseneeri*. The new species is also separated from the widespread *C. infundibulum* (Watson, 1879) by having a weaker P1 spiral cord and narrower umbilicus with spiral cords inside. The radula of the new species is also typically calliotropine.

Additional keywords: Seguenzioidea, deep-sea, methane seeps

INTRODUCTION

The genus *Calliotropis* is known to be very widespread and speciose: many new species, mainly from deep water, were described, e.g. from south western Indian Ocean (Vilvens, 2005, 2006), from the Philippines (Poppe et al., 2006), from Australia (Jansen, 1994), and from other areas of Indo-Pacific such as Taiwan, Indonesia, New Caledonia, Fiji and Vanuatu (Vilvens, 2004, 2007).

The deep-water malacofauna of the SE Pacific, and in particular that of Chile, is still poorly known. A survey of the Trochoidea including the description of two new species was recently presented by Vilvens and Sellanes (2006). The new species described in that work come from the bathyal zone (~850 m) Concepción Methane Seep Area (CMSA). This area has been proven to be a faunal aggregation "hotspot" that includes about 30 species of molluscs (Sellanes et al., 2008). Many of these species were previously unknown, mainly the chemosymbiotic bivalves and some of the gastropods (reviewed in Sellanes et al., 2008). Five species of the group Trochoidea inhabiting this seep area are currently identified to specific level: *Bathybembix macdonaldi* (Dall, 1890), *Margarites huloti* Vilvens and Sellanes, 2006, *Otukaia chilena* Rehder, 1971, *O. crustulum* Vilvens and Sellanes, 2006, *and Zetela alphonsi* Vilvens, 2002. An additional species of the group, collected in the vicinities of the same area and in 2001 off Antofagasta, was tentatively assigned to the genus *Calliotropis*. These latter constitute the first records for the genus from off Chile. The geographically closest records are those of Dell (1990), who described or reported some *Calliotropis* species from the adjacent Antarctic area (Ross, Weddell, and Bellingshausen seas).

The present paper aims to describe the new species of *Calliotropis* and to review the congeners for the Southeastern Pacific and adjacent Antarctic areas.

MATERIALS AND METHODS

Material of the present study consists of specimens obtained living (lv) from the dredge hauls performed by R/V Vidal Gormáz during the VG-07 cruise at two stations near the CMSA (~36° S). Additional material was collected off Antofagasta (22°48.02′ S, 70°36.71′ W) in 1350 m during 2001 in a R/V Sonne expedition. Abbreviations used are: H: shell height; W: shell width; HA: aperture height; TW: number of teleoconch whorls; spiral cords on teleoconch of the shells are labelled as P1, P2, ... etc., for primary cords (P1 being the most adapical) and S1, S2, ... etc., for secondary cords (S1 being the most adapical). Type specimens are deposited at Natural History Museum of Chile, Santiago (MNHNCL), Institut royal des Sciences naturelles de Belgique, Brussels, Belgium (IRSNB), and Muséum national d'Histoire naturelle, Paris, France (MNHN).

SYSTEMATICS

We follow herein the arrangement of Bouchet and Rocroi (2005) for the suprageneric allocation of

Calliotropis, although several authors still prefer to include the latter taxon in the Trochidae, as did Hickman and McLean (1990).

Superfamily Seguenzioidea Verrill, 1884
Family Chilodontidae Wenz, 1938
Subfamily Calliotropinae Hickman and McLean, 1990
Genus *Calliotropis* Seguenza, 1903

Type Species: *Trochus ottoi* Philippi, 1844 (by original designation) – Pliocene-Pleistocene, Italy.

Calliotropis ceciliae new species
(Figures 1–7, 15–19 Map 1, Table 1)

Description: Shell rather tall for genus (height up to approximately 17.5 mm, width up to 17.9 mm), slightly broader than high, rather thin, conical to weakly cyrtoconoidal; spire moderately elevated, height 0.92× to 0.98× width, 2.0× to 2.6× aperture height; umbilicus deep and narrow. Protoconch unknown (damaged in all available specimens).

Teleoconch of up to 6 convex whorls, bearing 3 spiral granular cords and prosocline threads; nodules produced by intersections of cords with axial folds on 3 first whorls; axial threads or folds not connecting nodules on last whorls. Suture visible, impressed, not canaliculated. First teleoconch whorl convex, sculptured by about 20 prosocline smooth riblets, interspace between riblets twice as broad as riblets; primary spiral cords P1 and P3 appearing at about mid-whorl, P3 slightly stronger than P1, both bearing rounded nodules produced by intersection with axial riblets; P2 absent. On second whorl, P1 and P3 stronger, P1 still weaker than P3; P4 appearing at end of whorl, partially covered by successive whorl, with beads smaller and more numerous than those of other cords. On third whorl, nodules of P1 and P3 stronger, slightly blunt sharp; beads of P1 oriented at 45°, beads of P3 horizontally oriented, slightly more numerous than those of P1; beads becoming nodules at end of whorl. On fourth whorl, nodules of P1 slightly stronger and less numerous than those of P3; beads of P4 much smaller and more numerous than those of other cords. On last whorl, P4 peripheral; periphery subangular; P1 weakening, sometimes almost obsolete, and P3 strongest; axial sculpture still visible, much stronger in upper part of whorl; S1 sometimes appearing intermediate between P1 and P3.

Aperture almost circular, with a weak, almost rounded angle at meeting of inner and outer lip; inner lip flanged in a curved arc projecting over umbilicus, partially covering it; parietal lip forming thin, transparent glaze. Columella more or less straight, without tooth, weakly prosocline. Base moderately convex, with 6 subgranular, similar by size, spiral cords; cords not evenly spaced, interspace between about twice to three times as broad as cords; very fine, poorly visible, axial, lamellate threads between cords. Umbilicus narrow, funnel-shaped, diameter 9–13 % of shell width, with very fine crowded axial lamellae and 2, sometimes 3, spiral cords within. Color of teleoconch pinkish ivory, without maculation. Operculum corneous, multispiral, with a short growing edge. Radula rhipidoglossate; formula ca. 12 + (1) + 3 + 1 + 3 + (1) + ca. 12. Rachidian tooth smaller than lateral teeth, with a small, hooded, not elaborately serrate cusp. Three lateral teeth per half row, similar in size and shape, with broad, hooded, serrated cusps. Lateromarginal plate present, with very rudimentary shaft and cusp. Marginal teeth thin, with long shaft and weakly serrated cutting edges; outermost marginal mitten-shaped.

Type Material: Holotype (MNHNCL 4158) (dd), AGOR Vidal Gormáz, stn AGT 06, from type locality; Paratype (MNHNCL 4159) (lv), paratype IRSNB (I.G. 31132) (dd), paratype MNHN (MNHN 21104) (dd), off Antofagasta, 22°48.02′ S, 70°36.71′ W, 1350 m; Paratype (MNHNCL 4160) (dd), AGOR Vidal Gormáz, stn AGT 07, 35°55.06′ S, 73°30.42′ W, 998-1128 m.

Type Locality: Central Chile, NW of Concepción, 35°31.48′ S, 73°22.71′W, 1100-1300 m, South Pacific Ocean.

Etymology: Named after Professor Dr. Cecilia Osorio, University of Chile, in recognition of her devotion to the study of mollusks, in particular the systematic, biological, and ecological aspects of the Chilean malacofauna.

Remarks: Two of the five available specimens of the new species (one of them being the largest) unfortunately lack their first whorls, giving only an estimated number of whorls. Also, some specimens from off Antofagasta are strongly eroded, making it difficult to count accurately the axial threads on the first whorls.

Calliotropis ceciliae new species is close to *C. pelseneeri pelseneeri* Cernohorsky, 1977 (Figures 8–10) from Antarctic seas, but the latter has a much more lamellose surface, a thicker P3 that angulates the whorl, a more convex base with more numerous spiral cords (the two outermost cords are closely spaced and separated from the other cords), and only a single spiral inside the umbilicus.

The new species weakly resembles *Calliotropis pelseneeri rossiana* Dell, 1990, but this subspecies has a P3 especially thick, a more angulate periphery and a subquadrangular aperture, giving a very different general shape to the shell.

Callitropis ceciliae new species may also be compared to *C. infundibulum* (Watson, 1879) (Figures 11–14) from western Atlantic, Indian-Atlantic Ridge and western Pacific, but this widespread species has a much stronger P1 cord, a wider umbilicus without a spiral cord inside, only 4 (sometimes 5) stronger spiral cords on the base.

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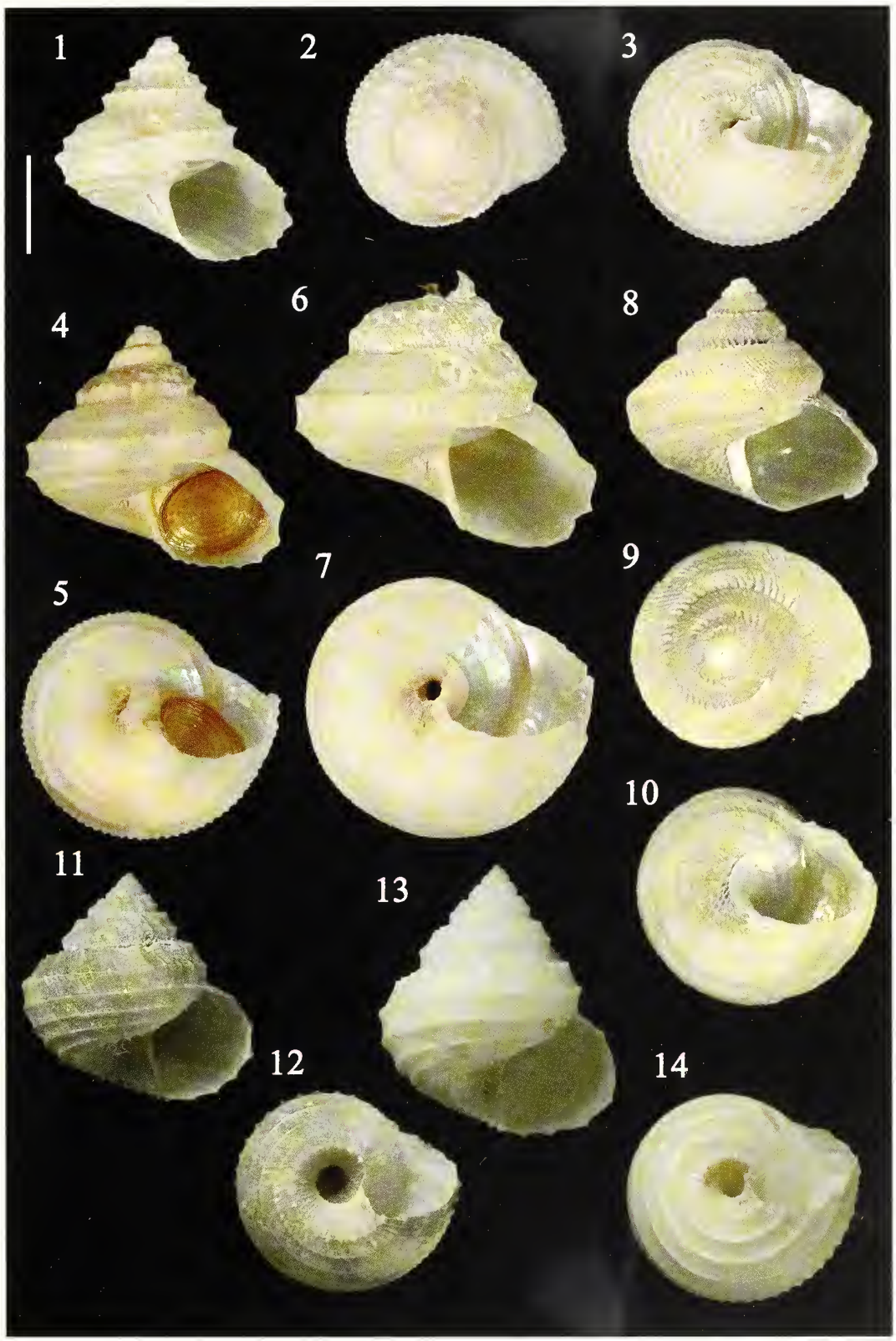
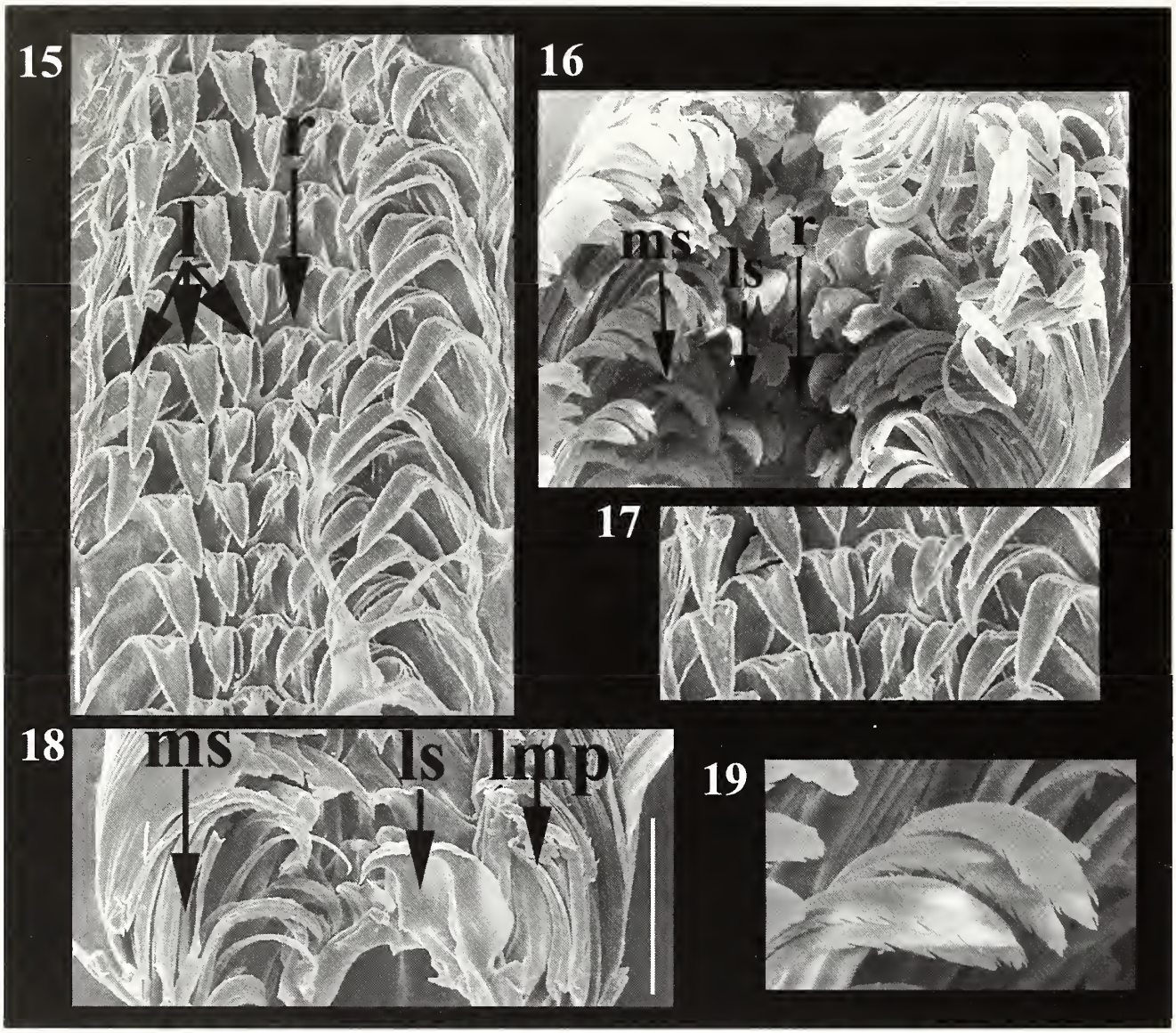


Figures 1–14. *Calliotropis* spp. **1–7.** *Calliotropis ceciliae* new species, Central Chile (scale bar = 5 mm.). **1–3.** Holotype MNHNCL (41584158), 10.4 x 11.3 mm. **4–5.** Paratype MNHNCL (4159), 12.1 x 13.1 mm. **6–7.** Paratype MNHNCL 4160, 17.5 (est.) x 17.9 mm. **8–10.** *Calliotropis pelseneeri pelseneeri* Cernohorsky, 1977, holotype USNM 612941, Weddel Sea, 11.0 x 12.1 mm – photos taken by Smithsonian National Museum of Natural History. **11–14.** *C. infundibulum* (Watson, 1879), syntypes BMNH, Prince Edward Island – photos taken by Phil Hurst (BMNH). **11–12.** BMNH (1887.2.9.325–7), 10.9 x 10.7 mm. **13–14.** BMNH (1887.2.9.328–9), 14.8 x 12.5 mm.



Figures 15–19. *Calliotropis ceciliae* new species, Central Chile (scale bar = 5 mm.), paratype MNHNCL (4159), features of the radula. **15.** Central field : rachidian (r) and lateral (ls) teeth. Scale bar = 100 µm. **16.** General view : rachidian (r), lateral (ls) and marginal (ms) teeth. Scale bar = 100 µm. **17.** Details of one row of the central field. **18.** Details of lateral (ls) and marginal (ms) teeth with lateromarginal plate (lmp). **19.** Details of marginal teeth.

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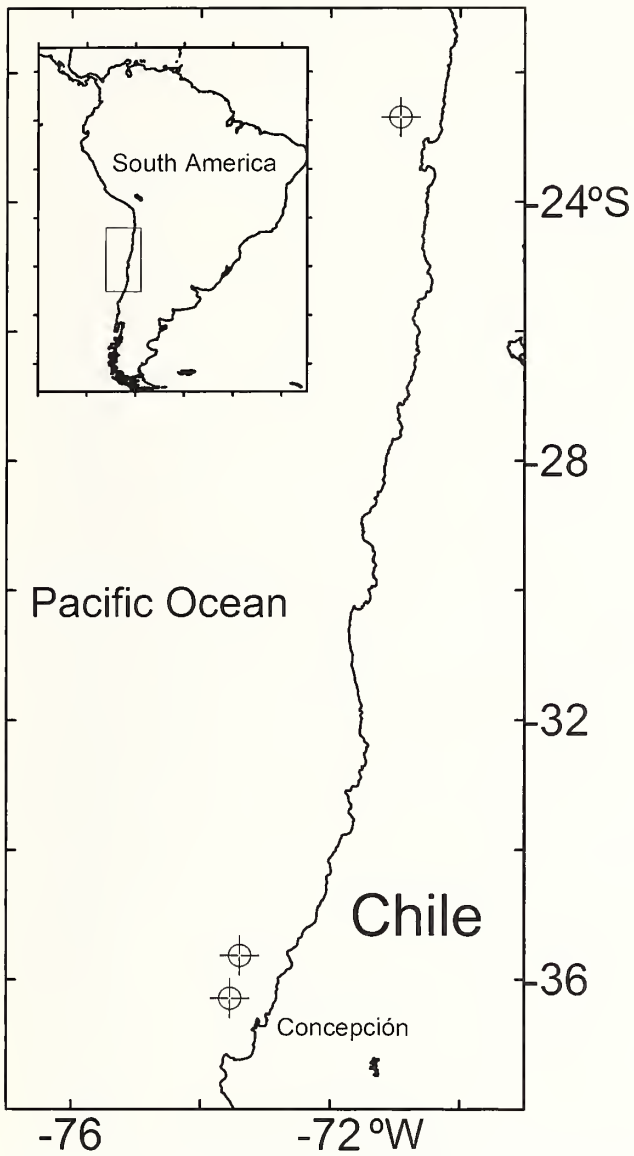
Table 1. *Calliotropis ceciliae*. Shell measurements (mm) of the types.

	TW	H	W	HA	H/W	H/HA
Holotype MNHNCL NW Concepción	5.0	10.4	11.3	4.8	0.92	2.17
Paratype MNHNCL Antofagasta	5.0	12.1	13.1	4.6	0.92	2.63
Paratype IRSNB Antofagasta	4.5	11.8	12.3	5.9	0.96	2.00
Paratype MNHN Antofagasta	4.0	10.7	11.3	5.1	0.95	2.10
Paratype MNHNCL NW Concepción (TW & H estimated)	6.0	17.5	17.9	7.5	0.98	2.33



Map 1. Map of the Chilean coast showing the locations off Antofagasta and NW off Concepción in which *Calliotropis ceciliae* new species has been collected.

institution, and P. Hurst and R.Miguez (BMNH) for the kind sending of photographs of the types of *Calliotropis infundibulum*. The pictures of *C. pelseneeri* were used with permission from the National Museum of Natural History, Smithsonian Institution, Washington, DC.

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A new *Scabrotrophon* (Gastropoda: Muricidae) from Hawaii and discussion about the generic classification of *Boreotrophon kamchatkanus* Dall, 1902, a related species

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ABSTRACT

A small muricid collected at 414 m off the Hawaiian Island of Oahu is described and compared, on the basis of shell characters only, with a syntype and two other specimens of *Scabrotrophon kamchatkanus* (Dall, 1902) (new combination) from the Northern Pacific. SEM images of the operculum, radula, and of the penis are illustrated for the new species.

INTRODUCTION

The discovery of a small murieid found with a sediment collector retrieved from 414 m in the Makapuu precious coral bed, situated in the channel between the islands of Oahu and Molokai in the Hawaiian Archipelago led to a note by Moffitt (2008: 16) and the seareh of its true identity. The species was first illustrated as "*Boreotrophon truncatus* (Ström, 1768) look alike", but further investigations proved it to be a new species closely related to *Scabrotrophon kamchatkanus* (Dall, 1902), an uncommon species from the North Pacific.

Abbreviations and Text Conventions: IP: Infrasutural primary cord (primary cord on sutural ramp); P1: Shoulder cord; P2–P6: Primary cords of the convex part of the teleoconch whorl; s1–s6: Secondary cords of the convex part of the telcoeoneh whorl; example: s1 = secondary cord betweeu P1 and P2; s2 = seeondary cord between P2 and P3, etc.; USNM: National Museum of Natural History, Smithsonian Institution, Washington, DC, USA; RH: collection of Roland Houart.

SYSTEMATICS

Family Muricidae Rafinesque, 1815
Subfamily Trophoninae sensu lato Cossmann, 1903

[1] Research Associate

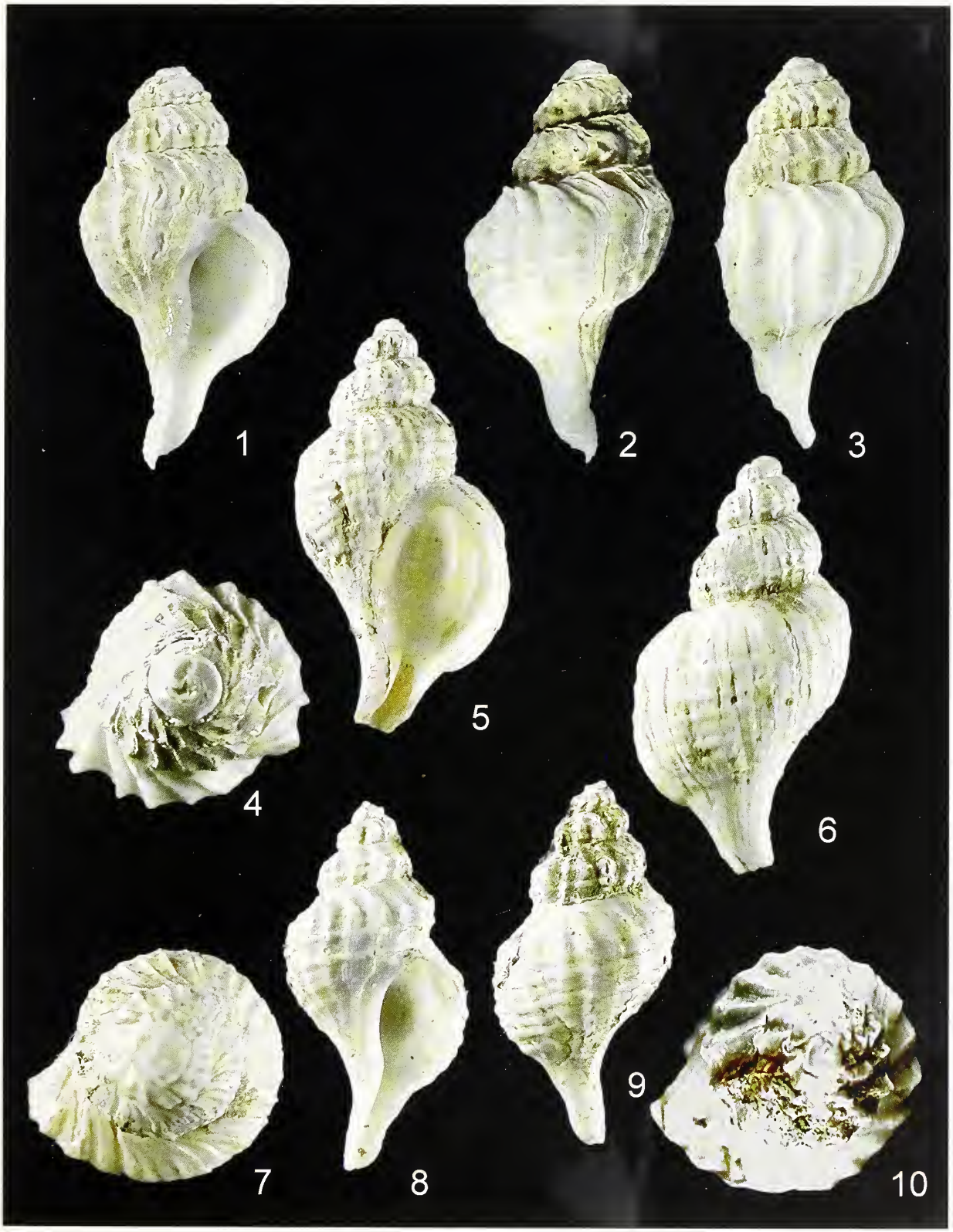
Genus *Scabrotrophon* McLean, 1996
Type speeies by original designation: *Trophon maltzani* Kobelt and Kuster, 1878, Northeastern Pacifie.

Scabrotrophon hawaiiensis new species
Figures 1–4, 14–17

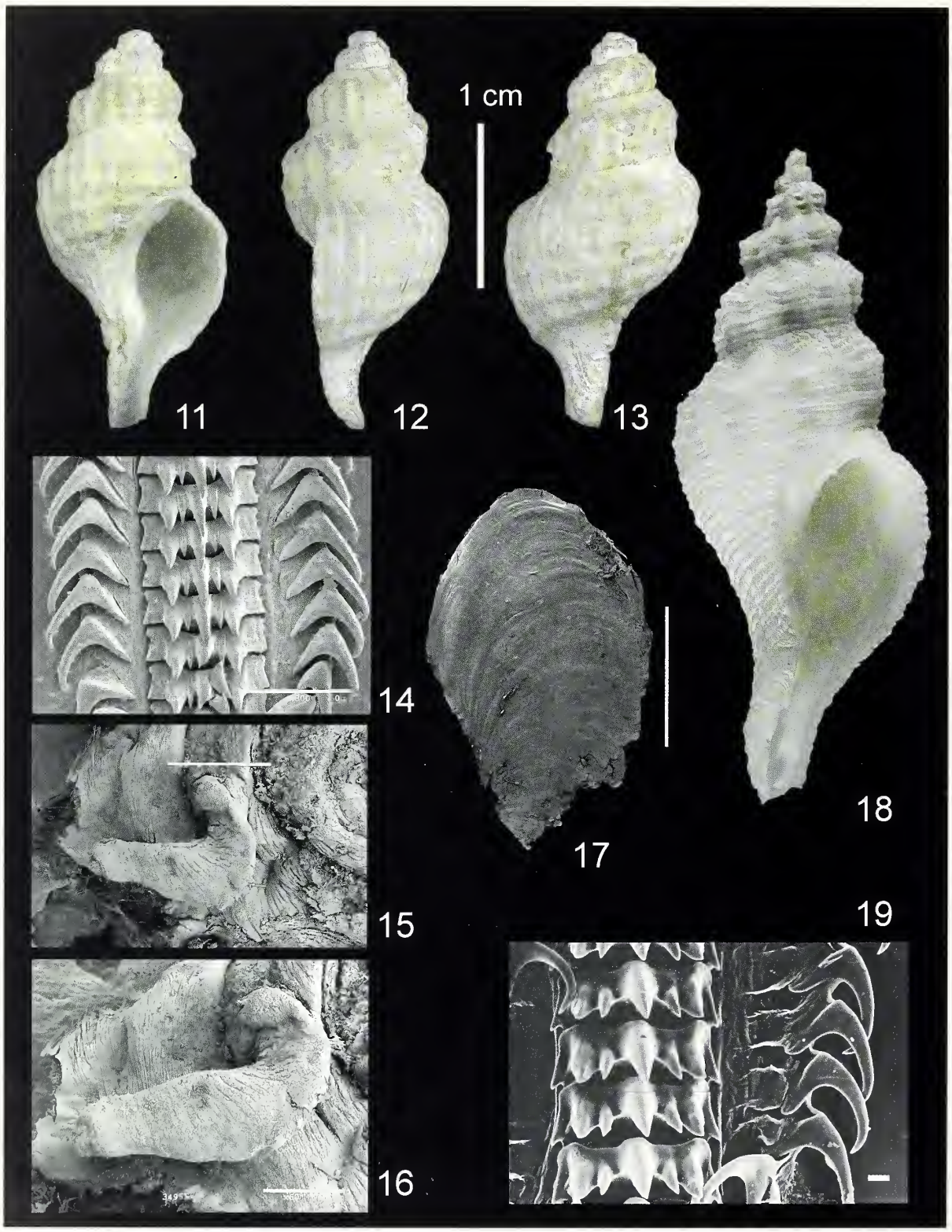
Boreotrophon truncatus (Strom, 1768) look alike—Moffitt, 2008: 7, text-fig.

Description: Shell medium-sized for the genus, holotype 18 mm in length. Width to length ratio 1.9:1. Bieonical, broad, heavy, lamellose. Shoulder strongly sloping, straight or weakly concave. Shell grayish-white, aperture glossy white. Spire high (teleoconch whorls 1 and 2 missing.) Axial seulpture of last teleoconch whorl consisting of 17 irregular, moderately high, strong, narrow lamellae, more strongly developed at sutural ramp, particularly near suture. Penultimate and ante-penultimate whorls with same number but lower, more regular lamellae. Previous whorl eroded, other whorls missing. Spiral sculpture of 6 low, weak, primary cords, more obvious on axial sculpture. Ontogeny unknown. Low IP, only visible at last portion of last teleoeonch whorl. Penultimate and antepenultimate whorls with P1 and P2. Sutural ramp smooth except axial lamellae. Aperture large, rounded-ovate. Columellar lip narrow, smooth, rim completely adherent. Outer lip of aperture smooth within. Siphonal canal moderately long, 36% of shell length, narrow, weakly abaxially bent at tip, broadly open. Operculum (Figure 17) inverted tear-shaped with apical nucleus and numerous concentrie ridges. Radula (Figure 14) with a raehidian tooth bearing a long, central cusp, a narrow, short, lateral denticle and a long, broad, lateral eusp. The lateral denticles are separated. Lateral cusp weakly broader and shorter than central cusp. Lateral teeth sickle-shaped with broad base. Penis small, broad, flattened, approximately 2 mm in length (Figures 15, 16).

Type Material: Holotype USNM 1137634



Figures 1–10. *Scabrotrophon* species. **1–4.** *Scabrotrophon hawaiiensis* new species, Makapuu Precious Coral Bed, 21°17.639′ N, 157°31.966′ W, with sediment collector, 414 m, 18 mm, Holotype USNM 1137634. **5–10.** *Scabrotrophon kamchatkanus* (Dall, 1902). **5–7.** California, off Trinidad, North of Eureka, 41°4′ N, 124°9′ W, dredged at 100–200 fms (183–366 m), 21.3 mm, coll. RH. **8–10.** California, off Eureka, 16.1 mm, coll. RH



Figures 11–19. *Scabrotrophon* species. **11–13.** *Scabrotrophon kamchatkanus* (Dall, 1902). Southeast coast of Kamchatka, 29 m, 25 mm, illustrated syntype USNM 109178 (photo courtesy Y. Villacampa, USNM). 14–17. *Scabrotrophon hawaiiensis* new species (SEM courtesy A. Warén). **14.** Radula. Scale bar = 50 µm. **15–16.** Penis. Scale bars: Figure 15 = 1 mm; Figure 16 = 500 µm. **17.** Operculum (scale bar 2 mm). **18–19.** *Scabrotrophon maltzani* (Kobelt and Kuster, 1878). 18. British Columbia, Egmont, dredged 31 m, coll. RH. **19.** Radula (scale bar 10 µm) (SEM A. Warén)

Type Locality: Makapuu Precious Coral Bed, 21°17.639′ N, 157°31.966′ W, collected with a sediment collector retrieved on Hawaii Undersea Research Laboratory Pisces V submersible dive P5-687, 414 m.

Distribution: Currently only known from the type locality.

Remarks: Another species of Trophoninae sensu lato, *Trophonopsis kayae* Habe, 1981, was described from deep water in Hawaii but it is not related to *S. hawaiiensis* new species and is more akin to *T. polycyma* Kuroda, 1953, from Japan and Fiji (Houart and Héros, 2008: 466). To our knowledge, only one species, living in the northeastern Pacific, *Scabrotrophon kamchatkanus*, is closely related. However, in *S. kamchatkanus* the spiral cords are comparatively broader and more strongly developed, obviously crossing the low axial lamellae. There are 5 primary spiral cords on the last teleoconch whorl in the holotype (P1–P5) with some secondary cords in other specimens examined [P1, s1, P2, s2, P3, (s3), P4, P5]. The penultimate and ante-penultimate whorls bear 3 or 4 cords, probably P1, s1, P2, (s2), the shoulder ramp is more slightly sloping in all specimens, and narrower. The axial lamellae in *S. kamchatkanus* are lower, occasionally almost indistinct, and the siphonal canal is shorter relatively to the height of the last telcoconch whorl. The operculum is less triangular, having a more ovate outline. The radula morphology and the penis are unknown in *S. kamchatkanus*.

Scabrotrophon kamchatkanus (Dall, 1902) **new combination**
Figures 5–10, 11–13

Boreotrophon kamchatkanus Dall, 1902: 541; Kosuge, 1972: pl. 8, fig. 6 (illustrated syntype).
Neptunea kamchatkana—Dall, 1921: 111, pl. 10, fig. 7 (syntype).
Trophonopsis kamchatkanus (var.)—Kuroda, 1953: 189; Tiba and Kosuge, 1985: 29, figs 1 (illustrated syntype), 2.
Trophonopsis kamchatkana—Higo et al.: 1999: 203; 2001: 62, fig. G2223 (illustrated syntype); Tsuchiya, 2000: 401, fig. 190.

Type Material: Illustrated syntype USNM 109178 (Figures 11–13); other syntypes USNM 635673 (Kantor and Sysoev, 2006: 148).

Type Locality: Dredged by the U.S. Fish Commission steamer *Albatross* on the southeast coast of Kamchatka, at station 3644, in 96 fms, shelly bottom, temperature 33°F (=0.6°C, Dall, 1902: 542). The depth of St. 3644 is erroneous. In checking the original publication, the depth was listed as 96 feet (which is 16 fathoms). This was transcribed as 96 fms on a label that had depth pre-printed in fathoms. It seems now clear that the correct depth for St. 3644 is 96 ft (= 16 fms or 29 m) (Harasewych, in litt.).

Other Material Examined: California, off Trinidad, North of Eureka, 41°4′ N, 124°9′ W, dredged at 100–200 fms (183–366 m), ex. R. Talmadge coll., coll. RH (Figures 5–7); off Eureka, ex. R. Talmadge coll., coll. RH (Figures 8–10).

Distribution: The Sea of Kashima-nada, Japan to the Bering Sea (Tsuchiya, 2000) and off Eureka, California (coll. RH), in 29–183 m. The maximum depth of 1495 m given by Tsuchiya (2000: 401) seems doubtful for living specimens.

DISCUSSION

The decision to include both species in *Scabrotrophon* is based on the shell morphology and the comparison with the type species of *Scabrotrophon* (Figures 18–19), a genus restricted to the Northern Hemisphere. As stated by McLean (1996: 93), the genus *Borcotrophon* is characterized by a dominant axial sculpture and the spiral sculpture (however rarely present in *Boreotrophon*) does not override the axial ribs. *Trophonopsis* has dominant axial sculpture in early whorls and the very prominent axial ribs of the type species *Trophonopsis muricatus* (Montagu, 1803) are overridden by spiral cords that form beads at intersection with the axial sculpture. Moreover the outer apertural lip is strongly denticulate in *Trophonopsis*. The generic allocation of other Northeastern "*Boreotrophon*" or "*Trophonopsis*" species probably needs to be reviewed.

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We are most grateful to M.G. (Jerry) Harasewych and Yolanda Villacampa (National Museum of Natural History, Smithsonian Institution) for the photographs of the syntype of *S. kamchatkanus*, to J. Harasewych for having solved the "mystery" of the depth of station 3644 (type locality). We are also most indebted to Anders Warén (Natural History Museum, Stockholm, Sweden) for preparation and SEM photographs of the radula, operculum, and penis of the new species. We also thank Dr. Frank Parrish (NOAA, PIFSC) who was the principal investigator on the Pisces V dive P5-687 as well as the Hawaii Undersea Research Laboratory and the staff and crews of the Pisces V and R/V Ka'imikai-o-Kanaloa, without whom this species would not have been collected. Finally we are very thankful to Yuri I. Kantor (Severtsov Institute of Ecology and Evolution of Russian Academy of Sciences, Moscow, Russia) for his useful remarks.

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Similar shells are not necessarily a reliable guide to phylogeny: *Rissoa guerinii* Récluz, 1843, and *Rissoa lia* (Monterosato, 1884) (Caenogastropoda: Rissoidae): a case study

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ABSTRACT

According to the recent theory of speciation through loss of planktotrophy, the pairs of northeastern Atlantic species of caenogastropods would be the result of a cladogenetic event in which a planktotrophic ancestor gave rise to two geographically separated species with different modes of larval development, but retained virtually identical teleoconch characters. This idea was proposed as the working hypothesis for the origin of the pair of supposed sibling species *Rissoa guerinii* Récluz, 1843 and *R. lia* (Monterosato, 1884). The present study shows that claims of a close morphological resemblance between the two species are unjustified as a considerable divergence emerged in shell geometric morphometric analysis and in 16S rRNA mitochondrial gene. We conclude that *R. guerinii* and *R. lia* cannot be regarded as sister or cryptic species and should no longer be considered a planktotrophic/non-planktotrophic pair.

Additional keywords: Gastropoda, sibling species, larval development strategy, mitochondrial DNA, geometric morphometry

INTRODUCTION

Many authors (e.g. Jablonski and Lutz, 1983) identified two main categories of developmental strategies in marine invertebrates: planktrotrophy (P), with larvae feeding on plankton, and non-planktotrophy (NP), with planktonic larvae feeding only on their yolk supply (lecithotrophy), or with direct development.

According to the so-called "shell-apex rule" (Thorson, 1950), larval development in marine gastropods can be inferred from observations of the protoconch. A multispiral protoconch and a smaller dimension of the initial whorl accounts for a planktotrophic developmental mode, whereas a larger paucispiral protoconch is directly linked to non-planktotrophy.

There are several examples of northeastern Atlantic caenogastropod pairs of related taxa that possess identical teleoconchs and differ exclusively in protoconch characters. Oliverio (1996) provided a list of 28 of these P/NP pairs and indicated that their specific status is still a matter of debate.

Verduin (1986) maintained that in species of *Rissoa* (Rissoidae) the occurrence of this phenomenon is of remarkable extent and nine pairs of Oliverio's list were species of this genus. In his revision of the genus, Verduin (1976, 1982, 1985, 1986) considered differences in developmental mode to definitively separate species, thus regarding each member of a P/NP pair as a distinct species. His opinion was commonly accepted (e.g. Bouchet, 1989), although some authors have more recently suggested the possibility of intraspecific variability in larval development (Warén, 1996; Cadèe, 1998) or that this variation indicated incipient speciation (Rehfeldt, 1968; Panico and Patti, 2005).

Oliverio (1996) suggested a mechanism of speciation explaining the origin of P/NP pairs in the NE Atlantic region. This involved the modification of larval development, with one species abandoning planktotrophic feeding, thus giving rise to another species. From the observation that in the Mediterranean the non-planktotrophic mode is more dominant in the Eastern basin, Oliverio (1996) suggested a paleogeographic model to explain the reasons of speciation through the loss of planktotrophy. During glacial periods sea level lows caused isolation between the Mediterranean and the Atlantic, and between the Eastern and Western Mediterranean basins. The resulting conditions gave rise to factors thought to select against planktotrophic larvae (fluctuations in the energy input, restricted areas, and higher predation pressure; Strathmann, 1978a, b). These factors may have caused the shift from planktotrophy to lecitotrophy resulting in speciation and origin of a P/NP pair.

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Within this scenario, species forming a P/NP pair can be considered sibling species (sensu Knowlton, 1986), being both cryptic (i.e., difficult to distinguish using the traditional morphological characters) and sister (i.e., sharing the same ancestor).

After the examination of a large amount of museum material of *Rissoa guerinii* Récluz, 1843, and *Rissoa lia* (Monterosato), 1884 (Rissoidae), Verduin (1985) highlighted a strong resemblance in shell characters between these species and concluded that they "may often only be identified reliably by their type of apex" (Verduin 1986: 14). Their distribution (Verduin, 1985) overlaps in the Western Mediterranean, but only *R. guerinii*, occurs in the Atlantic and is absent from the Adriatic and Aegean, where *R. lia* is present.

In this work we provide, based on both dry and live-collected material, a critical reinterpretation of the two taxa and investigate their phylogenetic relationships.

MATERIALS AND METHODS

The source of the biological material examined in this study is twofold. Snails from field sampling and empty shells belonging to the historical collection of Philippe Dautzenberg (housed in the Royal Belgian Institute of Natural History (RBINS), Brussels) have been used in this research.

Live-collected Material

Sampling of living material was performed in the infralittoral of Santa Tecla, Sicily (Mediterranean, Ionian Sea), where both species commonly occur (Scuderi, pers. comm.), at 1–5 m depth in Dec. 2005, Apr., Jun., and Nov. 2006. About 0.03 m^3 of the red alga *Pterocladiella capillacea* (S. G. Gmelin) Santelices and Hommersand was collected by SCUBA diving for each sample. Material was immersed in seawater and transferred to the laboratory. Each sample was divided into 20 subsamples that were individually washed in a tank containing 5 l of 50% seawater for not more than five minutes. Osmotic shock provided caused the vagile fauna to detach from the algal thallus and fall in the bottom of the tank, from where the specimens were quickly collected and placed in seawater. Living material was sorted and taxonomically determined under a Wild Makroskop M420 stereoscopic microscope. Specimens belonging to *Rissoa guerinii* and *R. lia* were isolated; their sex was determined by checking the presence of a penis in the right side of pallial cavity. Some were placed separately in running seawater at 18°C and provided with fresh *P. capillacea* thalli, others were immediately preserved in 80% ethanol. Reared specimens did not survive more than 6 weeks; empty shells of dead specimens were retained and used for observation.

Shells and Head-foot: Adult living specimens of both *R. guerinii* and *R. lia* were placed in a Petri dish with seawater. Shells were held with forceps and the snails attempted to crawl extending their foot completely, enabling the head-foot to be observed in detail. Images were taken and digitized using a Leica DFC 300 FX video camera and Leica Application Suite version 2.4.0 software. Color drawings were also made to better represent the color pattern of the head-foot.

Traditional Shell Morphometry: Standard teleoconch (L, M, W_{N-1}, D_{N-1}) and protoconch parameters (d and D_0) (Verduin, 1982a) were measured on a sample of 100 randomly selected shells (from 53 males and 47 females) from live-collected material of each species. The total number of shell whorls (N) was also counted. The following standard teleoconch ratios were calculated: relative height (L/N), slenderness (L/D_{N-1}), relative aperture height (M /L) and last-whorl height over width ratio (W_{N-1}/ D_{N-1}).

A principal component analysis (PCA) and a discriminant analysis (DA) were performed on the dataset obtained combining protoconch parameters and teleoconch ratios. Tests and plots were implemented by SPSS v.15 statistical software (© SPSS Inc., 2006) and by SYSTAT statistic software v. 12 (Wilkinson et al., 1992).

Geometric Shell Morphometry: Fifteen shells (8 females and 7 males) at terminal growth were randomly selected from live-collected material of each species. Shells were observed using a Leica Z16 APO stereoscopic microscope, and colour images were taken and digitized using a Leica DFC 300 FX video camera and Leica Application Suite version 2.4.0 software. The shells were always placed in the same position, with the coiling axis in vertical position and the aperture on the same plane as the objective (Carvájal-Rodríguez et al., 2005). Using the software tpsDIG2 v. 2.10 (Rohlf, 2007a), 19 landmarks (LM) were established (Figure 1). LM1 is the apex of the shell; LM2, LM4 and LM6 are placed on the right border of the profile at the beginning of the three last complete whorls. LM15, LM17, and LM19 are the corresponding landmarks on the left border of the profile. LM3, LM5, LM16, and LM18 mark the intermediate position respectively between LM2 and LM4, LM4 and LM6, LM15 and LM17, LM17, and LM19 along the curvature of the whorl; LM8 is at the lower suture of the last complete whorl and LM7 marks the intermediate position between LM6 and LM8 along the curvature of the whorl. LM9 is the most external position in the upper part of the outer lip; LM10 and LM12 are the most external positions respectively in the external right and left part of the outer lip; LM11 is the lowest point at the base; LM14 is the most external point in the last whorl at the left profile of the shell; LM13 is the profile point between LM12 and LM14 (closest to LM7). As described in Carvájal-Rodríguez et al. (2005) the matrix of raw coordinates generated by tpsDIG2 was used in tpsRelw v.1.45 (Rohlf, 2007b) to compute shell size (CS), uniform (U1 and U2) and non-uniform (several relative warps, RWs) shape components for each specimen. Standard

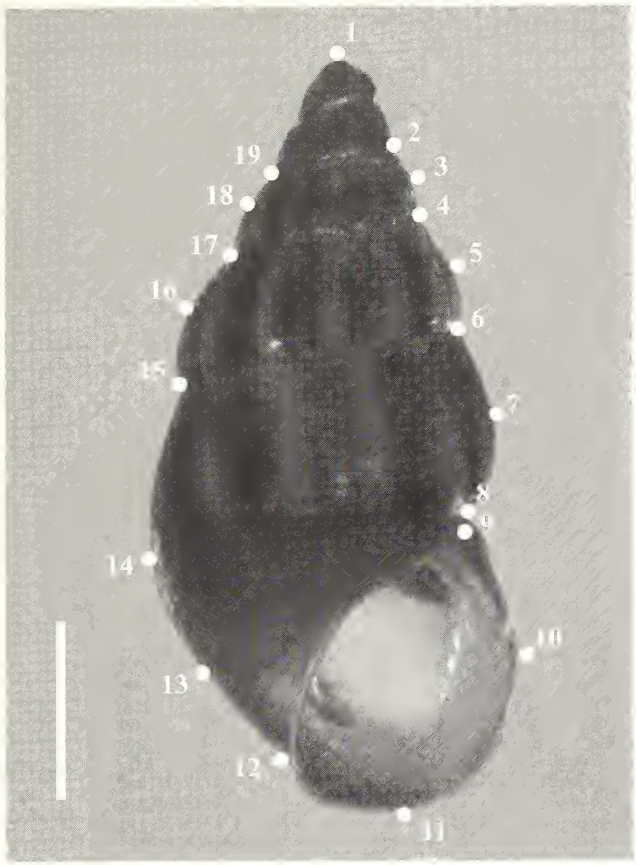


Figure 1. Shell of a live-collected *R. lia* from S. Tecla showing the placement of the 19 landmarks used for geometric morphometric analysis. Scale bar = 1 mm.

parametric tests were performed on the obtained variables using the SPSS/PC package v. 15.0.

Radular Analysis: The shell of 10 live-collected specimens of each species was removed and the bodies incubated for 3–4 hours at 50°C in 70% KOH solution. After complete tissue dissolution, radulae were isolated, rinsed in distilled water, and mounted on SEM stubs. Observation and pictures were made using a Jeol JSM-6700F scanning electron microscope. The cusps of rachidian and lateral teeth were counted and frequency histograms were drawn to show differences in cusps arrangement between the two species.

Molecular Systematics: Forty-five ethanol preserved specimens of *R. guerinii* and 34 of *R. lia* were randomly selected from live-collected material. The shell of each specimen was broken in a mortar and removed. DNA extraction plus amplification, purification and sequencing of a 337 bp segment of mitochondrial 16S rRNA gene were performed as described in Criscione et al., 2009.

Sequences obtained were aligned with CodonCode Aligner v. 1.6.3 (CodonCode Corporation, Dedham, MA) and the alignment refined by eye. For all samples, both forward and reverse strands were analysed. Genbank accession numbers for sequences used in the analysis are given in Table 2.

For the sequences generated, Parsimony and Maximum likelihood trees were obtained using PAUP* v. 4.04 (Swofford, 2003). The program Modeltest version 3.06 (Posada and Crandall, 1998) was employed to select HKY+I model in Maximum Likelihood. In computing trees, the option of 1000 bootstrap replicates was selected. A reduced median joining network (MJ) (Bandelt et al., 1999) was obtained with the software Network v. 4.5 (http://www.fluxus-technology.com/NETW4500.exe).

Table 1. List of studied material in Dautzenberg collection (RBINS).

Acronym	No. of shells contained	Main original label
Rga	About 80 *R. guerinii*	*Rissoa guerini* Recl. var. *albina* Dautz./Rochebonne/dd. 16.IX.05
Rgb	About 60 *R. guerinii*	*Rissoa guerini* Recl. var. *bipartita* Dz and Dur./Rochebonne/dd. 16.IX.05
Rgc	About 80 *R. guerinii*	*Rissoa guerini* Recl. var. *conspersa* Dautz. and Durouchoux/ Rochebonne/dd. 16-IX.05
Rlma	Many *R. lia*	*R. (Apicularia)* lia, Benoit/typique de Messina!/Monterosato 2.III.17
Rlmb	5 *R. lia*	bis/R. (*Apicularia*) lia, Benoit/ Messina! Playa
Rlp	8 *R. lia*	*Rissoa lia* Monts./Paulille/Bucquoy
Rlt	many *R. lia*	*Rissoa lia* Benoit/Tanger/Pallary 1. 7. 98

Table 2. GenBank accession numbers for the sequences used in the analysis. Accession numbers with the prefix GU were collected for this study.

Taxon	AN	Analysis
R. guerinii	from GU177882 to GU177921	NJ, MP, ML, MJ
R. lia	from GU177922 to GU177955	NJ, MP, ML, MJ
R. similis	GU177963	NJ, MP, ML, MJ
R. labiosa	AY676117	NJ, MP, ML, MJ
R. parva	AF445343	NJ, MP, ML, MJ
R. auriscalpium	GU177879	MJ
R. variabilis	GU177880	MJ
R. violacea	GU177881	MJ

Dautzenberg Collection Material

The relevant material in the Dautzenberg collection was examined using an Olympus® SZX10 stereoscopic microscope. After this survey, 15 lots were selected as on their historical value as vouchers (Verduin, 1985) and the specific determination of the shells contained

was verified according to current taxonomy. Clearly misclassified specimens in the lots were temporarily removed and not further considered. Several specimens of each lot were observed using the stereomicroscope and digital pictures were taken with an Olympus® CAMEDIA C-7070 WZ digital camera. Table 1 contains the list of the lots studied, accompanied by the data on the original label, the number of specimens present and photographed, and their revised species determination. An acronym is given to enable identification of the lot in the following text.

RESULTS

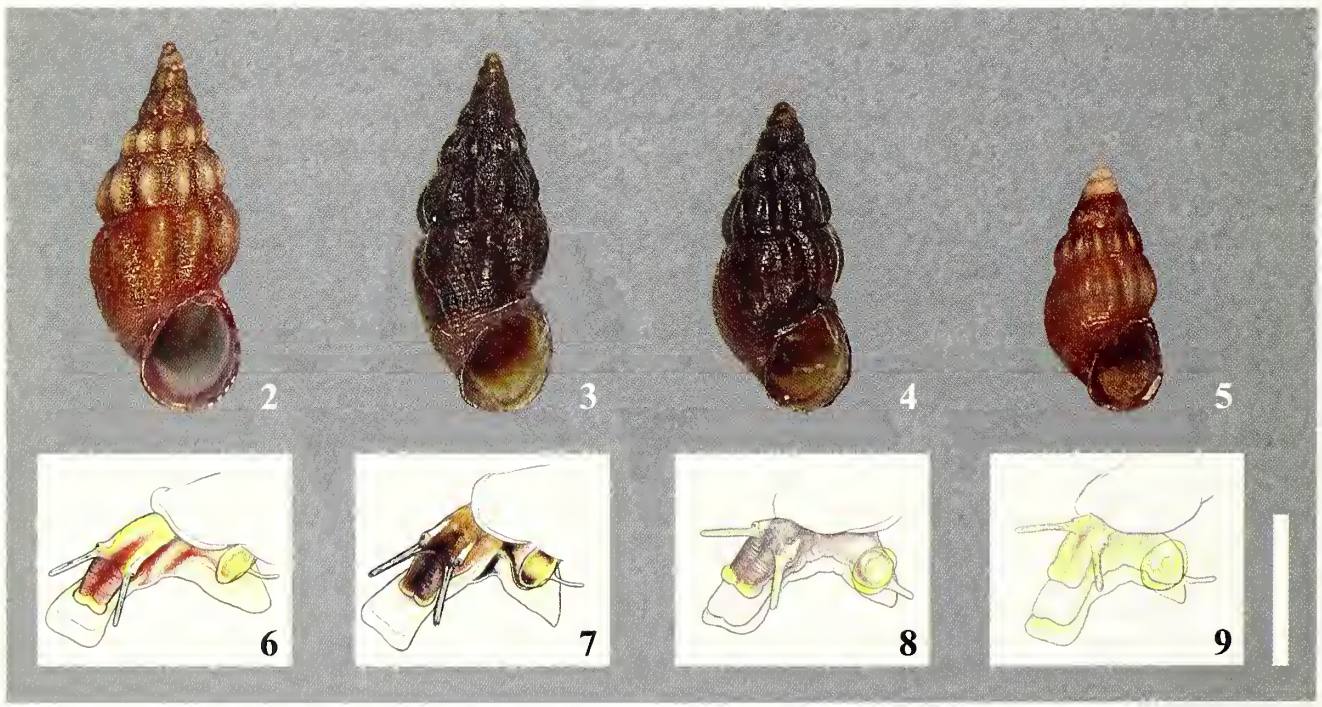
Live-collected Material

***Rissoa guerinii* Shell:** Shell spindle-shaped; apex solid, sharp and glossy; whorls 7, apical 2–3 nearly flat-sided, 3–4 youngest ribbed and more convex, with penultimate whorl generally bulging out and giving shell characteristic fusiform shape. Shells of females always bigger than those of males with same number of whorls.

Shell ornamentation composed by axial ribs and intervening furrows, spiral ridges and intervening grooves, and growth lines. Shells devoid of spiral ornamentation rarely found. Axial ribs limited to youngest 3–4 whorls, 11–14 per whorl, robust and prominent, swelling in middle of whorl and fading toward shell base; normally slightly opisthocline, tending to prosocline on body whorl near aperture and close to suture being slightly flexuous; each rib equal in breadth to interspaces. Extremely weak labral rib, often having appearance of whitish smudge as broad as two axial ribs, starting from end of last axial rib and ending before outer lip. Spiral ridges with grooves delicately and closely cancellated as a result of intersection with growth lines. Growth lines prosocline and running obliquely over ribs and furrows. Aperture as described by Fretter and Graham (1978). Two distinct shell colour varieties detected: typical and "var. *conspersa*" (Dautzenberg and Durouchoux, 1914). Typical *R. guerinii* (Figure 2) with ribless white-brownish or lilac whorls, youngest showing sinuous brown spiral lines corresponding to furrows of ribbed whorls. Ribless whorls with fawn or brown background colour on furrows among ribs and on shell base (sometimes tinged pale lilac up to base of ribs). A checkerboard pattern (or a series of zigzag lines) created by background color and a whitish color occasionally present. Ribs always whitish or pale lilac. Peristome pale violet, throat with brown-lilac band extending on to columella.

Rissoa guerinii "var. *conspersa*" (Figure 3) with entire shell covered by a uniform chess board pattern or a series of zigzag lines (as described for some typical shells), with predominance of a dark brown colour over whitish colour. Ribs often encircled by a white line, normally interrupted in correspondence of intervening furrows. Apex, peristome, and inner part of aperture as described for typical pattern.

***Rissoa guerinii* Head-foot:** As for shells, two colour types detected (Figure 6, 7), viz. typical *R. guerinii* and *R. guerinii* "var. *conspersa*" (Dautzenberg and



Figures 2–9. Pictures of shells and drawings of soft body parts of *R. guerinii* typical (2, 6), *R. guerinii* "var. *conspersa*" (3, 7), *R. lia* "var. *castanea*" (4, 8) and *R. lia* "var. *fulva*" (5, 9). Scale bar = 1 mm. Drawings by D. Scuderi.

Durouchoux, 1914). Foot always whitish and median part of sole stained brown, lighter in typical *R. gnerinii* than in "var. *conspersa*." Snout light brown in *R. gnerinii* typical and darker brown in "var. *conspersa*." Margins of distal portion of snout and remaining part of head yellowish in *R. gnerinii* and light brown in "var. *conspersa*." Cephalic tentacles whitish, but sometimes dark brown in "var. *conspersa*." A whitish spot behind base of cephalic tentacles always present.

***Rissoa lia* Shell:** Shell conical, apex solid, obtuse and opaque; whorls 6, all equal-sided and tumid, apical 2 whorls ribless, others ribbed or ribless (though last whorl often ribless), penultimate generally not bulging out rest. Sexual dimorphism as for *R. gnerinii*. Shell ornamentation of axial ribs and intervening furrows, spiral ridges and intervening grooves, and growth lines. No shells devoid of spiral ornamentation found. Axial ribs (when present) always 14 per whorl, strong and prominent, with same thickness across whorl but fading towards base on body whorl; normally slightly opisthocline, tending to be prosocline; each rib slightly narrower than intervening furrow. No labral rib or whitish smudge before peristome present. Spiral ornamentation as for *R. gnerinii*. Aperture oval or D-shaped, peristome not showing sinuses or slight projection of inner lip; edge very thin, beveled internally turning out to form a though thin flange. Outer lip arising below periphery of body whorl, (somewhat below level at which ribs end), its curvature initially slight or sometimes nearly straight. Columella short, peristome everted over a groove, no umbilicus present. Two distinct color varieties detected, here named *castanea* and *fulva* (after Monterosato, 1884). Intermediate specimens rarely found. *R lia* "var. *castanea*" (Figure 4) violet-brownish to dark brown with ribs always lighter. First two whorls white but sometimes brown to dark brown. Peristome violet-brownish. *R. lia* "var. *fulva*" (Figure 5) uniformly fawn with ribs always lighter or even whitish. First two whorls fawn or white. Peristome as in "var. *castanea*", but neck with a brown-lilac band running from lower border of labral rib to columella.

***Rissoa lia* Head-foot:** As for *R. gnerinii*, two different color types detected remarkably distinct in colour pattern and corresponding to shell colour variety and thus named *castanea* and *fulva* (Figures 8, 9). Foot always entirely whitish and cephalic tentacles always yellowish with a whitish spot behind their base. In *R. lia* "var. *castanea*" snout dark and its distal part yellowish, in "var. *fulva*" snout yellowish, often with a short brownish stripe running along median part.

Traditional Morphometry: Among the 6 principal components extracted, PC1 (55%) and PC2 (26%) explained most of the variance observed (Table 3). Component matrix (Table 4) and loading plot (Figure 10) illustrate the correlation between principal components and shell variables. PC1 is a strongly positively correlated with L/N, L/D_{N-1} and W_{N-1}/ D_{N-1}, strongly negatively correlated with M/L and weakly negatively correlated with d and D_0. PC2 is not significantly correlated with teleoconch ratios but it is strongly positively correlated with d and D_0.

No clear clusters resulted from plotting PC1 value of each shell against its respective PC2 value (Figure 11). The 95% confidence ellipse of *R. gnerinii* contains almost only positive values of PC1, but both positive and negative values of PC2 whereas that of *R. lia* encircles mostly negative values of both PC1 and PC2.

The eigenvalue of discriminant function between the two species was 1.307, the canonical correlation 0.753 and the Wilks' lambda (0.433) was highly significant ($p<0.001$). The structure matrix (Table 5) shows the cumulative within-groups correlations between discriminating shell variables and the standardized canonical discriminant function obtained. Table 6 shows the results of the classification statistics obtained using the values of the discriminant function of each individual to predict its *a posteriori* species membership.

Geometric Morphometry: Table 8 shows the percentages and a descriptive statistical summary of the

Table 4. Component matrix for the first two principal components.

	Component	
	1	2
D	–0.271	0.864
D_0	–0.318	0.848
L/N	0.843	0.181
L/D_{N-1}	0.914	0.134
M/L	–0.913	–0.151
W_{N-1}/ D_{N-1}	0.860	0.106

Table 3. Total variance explained by single principal components.

	Initial Eigenvalues			Extraction Sums of Squared Loadings		
Component	Total	% of Variance	Cumulative %	Total	% of Variance	Cumulative %
1	3.294	54.901	54.9	3.294	54.901	54.9
2	1.551	25.852	80.8	1.551	25.852	80.8
3	0.432	7.193	87.9			
4	0.342	5.704	93.6			
5	0.235	3.909	97.6			
6	0.147	2.442	100.0			

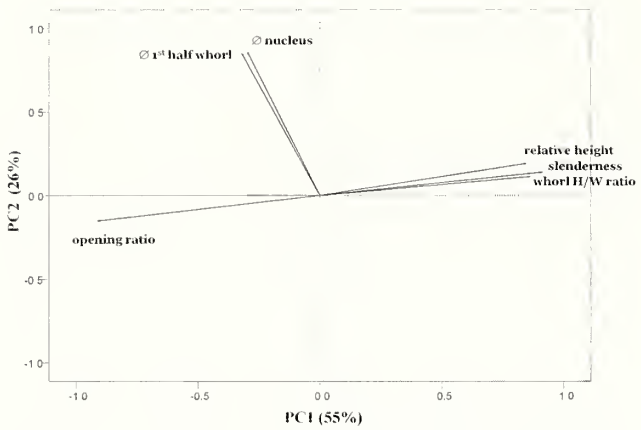


Figure 10. Loading plot of the shell variables relative to the first two principal components.

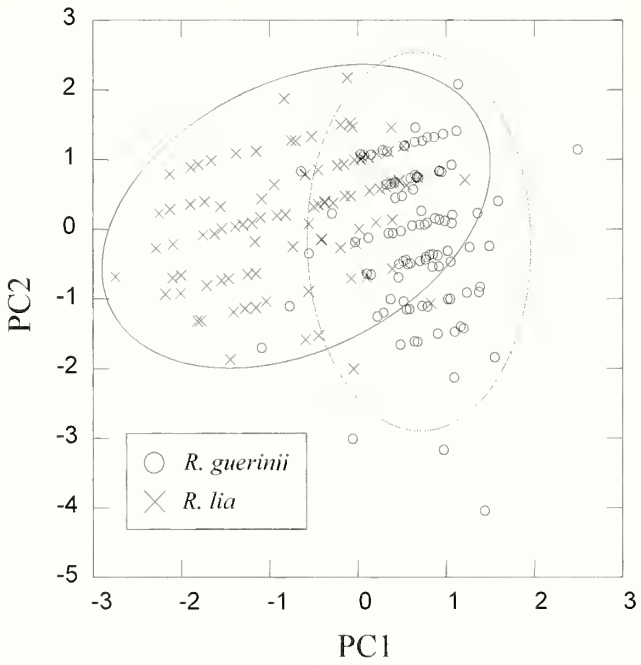


Figure 11. Scatterplot of the first two principal components. 95% confidence ellipses are drawn for each species. Dashed ellipse represents *R. guerinii*.

Table 5. Structure matrix showing the loadings of each shell variable on the discriminant function. The variables are ordered by absolute size of correlation within discriminant function.

	Discriminant Function
M/L	0.717
L/N	–0.699
L/D_{N-1}	–0.672
W_{N-1}/ D_{N-1}	-0.487
d	0.382
D_0	0.307

Table 6. Classification summary for the discriminant analysis.

Species		*R. guerinii*	*R. lia*	Total
Count	*R. guerinii*	93	7	100
	R. lia	14	86	100
%	*R. guerinii*	93.0	7.0	100.0
	R. lia	14.0	86.0	100.0

Table 7. Multiple regression model testing allometry for the non-uniform shell shape variables.

Multiple regression		Variables in the model	
r^2	F	Name	Beta
0.5	20.3^{***}	RW2	-0.648^{***}
		RW9	0.282^{**}

$^{**}P < 0.05$, $^{***}P < 0.001$.

relative score for CS, the two uniform components and the first 10 RWs, explaining more than the 91% of the overall variation. Table 7 shows the results of the allometric analysis for shell shape measurements conducted by step-wise multiple regression analysis for centroid size (as dependent variable) and two uniform and 29 non-uniform measurements, as independent variables. The F test of the regression analysis was highly significant ($p<0.001$) and two of the relative warps, RW2 and RW9, contributed significantly to the regression model on the centroid size. Centroid size, uniform components and only the first ten relative warps were considered in the analysis of variance (ANOVA), performed to evaluate the significance of differences in size and shape variables. Shells of *R. guerinii* and *R. lia* differed significantly in CS ($p<0.001$), RW1 ($p<0.05$) and RW2 ($p<0.05$). The cumulative results of the analysis are shown in Table 8. The significance level obtained for the corrected analysis (ANCOVA) with centroid size as covariate was not maintained for the difference in RW1, but was not affected for RW2. The eigenvalue of the stepwise discriminant function between the two species, calculated for the 29 RWs, was 3.199, the canonical correlation 0.873 and Wilks' lambda (0.238) was highly significant ($p<0.001$), indicating a good separation between groups. Twelve shape variables contributed to the discriminant function (RW1, RW2, RW4, RW5, RW6, RW7, RW9, RW10, RW18, RW23, and RW27). The standardized coefficient matrix (Table 9) shows the relative importance of the independent variables in determining the standardized canonical discriminant function. Using the individual values of the discriminant functions to predict *a posteriori* species memberships, 26 (86.7%) individuals out of 30, were assigned to the correct species, leaving only 4 (13.3%) that were erroneously classified. Looking at species statistics (Table 10), 13 (86.7%) specimens of *R. guerinii* were correctly assigned to this species and only two (13.3%) were assigned to *R. lia*. The same percentages of correctly/

Table 8. Descriptive statistical summary and results of ANOVA and ANCOVA for the main shell size and shape variables between *R. guerinii* and *R. lia*. **P < 0.05, *** P < 0.001, ns = non significant.

Measure		CS	U1	U2	RW1	RW2	RW3	RW4	RW5	RW6	RW7	RW8	RW9	RW10
Variance explained					32.2%	19.4%	14.5%	8.2%	4.2%	3.6%	3.2%	2.5%	2.0%	1.9%
R. guerinii	Mean	1020	–0.001	0.001	0.012	–0.011	–0.002	–0.004	–0.003	0.003	–0.003	0.000	0.002	–0.001
	SD	122	0.014	0.010	0.038	0.016	0.025	0.018	0.012	0.010	0.010	0.010	0.009	0.008
R. lia	Mean	815	0.001	–0.001	–0.012	0.011	0.002	0.004	0.003	–0.003	0.003	0.000	–0.002	0.001
	SD	128	0.012	0.009	0.016	0.026	0.017	0.012	0.010	0.010	0.009	0.008	0.006	0.007
ANOVA		20.10***	0.11 ns	0.45 ns	4.79**	7.97**	0.32 ns	2.05 ns	2.42 ns	1.96 ns	2.16 ns	0.06 ns	3.43 ns	0.75 ns
ANCOVA			1.06 ns	0.46 ns	3.21 ns	9.96**	0.20 ns	1.00 ns	1.38 ns	1.19 ns	1.57 ns	0.15 ns	1.79 ns	2.01 ns

Table 9. Standardized coefficient matrix showing the relative importance of the shape variables.

	Discriminant function
RW2	1.501
RW1	–1.276
RW9	–1.127
RW5	0.978
RW7	0.932
RW4	0.911
RW6	–0.893
RW23	–0.789
RW27	0.716
RW18	–0.685

Table 10. Summary of classification results obtained employing the discriminant function.

Species		*R. guerinii*	*R. lia*	Total
Count	*R. guerinii*	13	2	15
	R. lia	2	13	15
%	*R. guerinii*	86.7	13.3	100.0
	R. lia	86.7	13.3	100.0

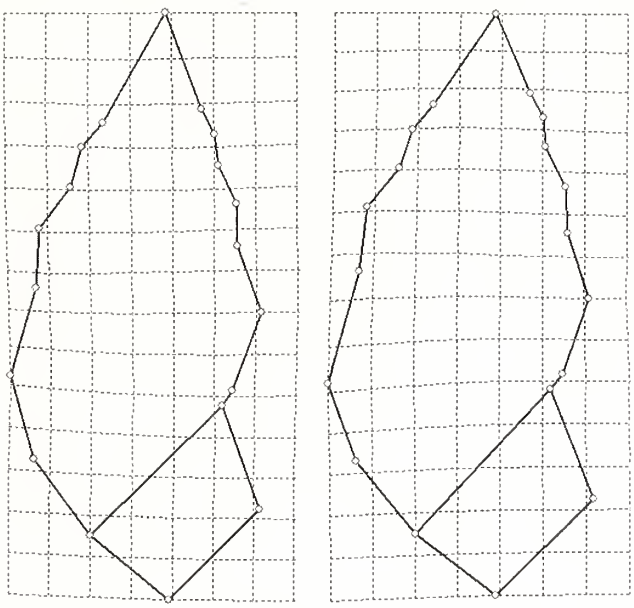


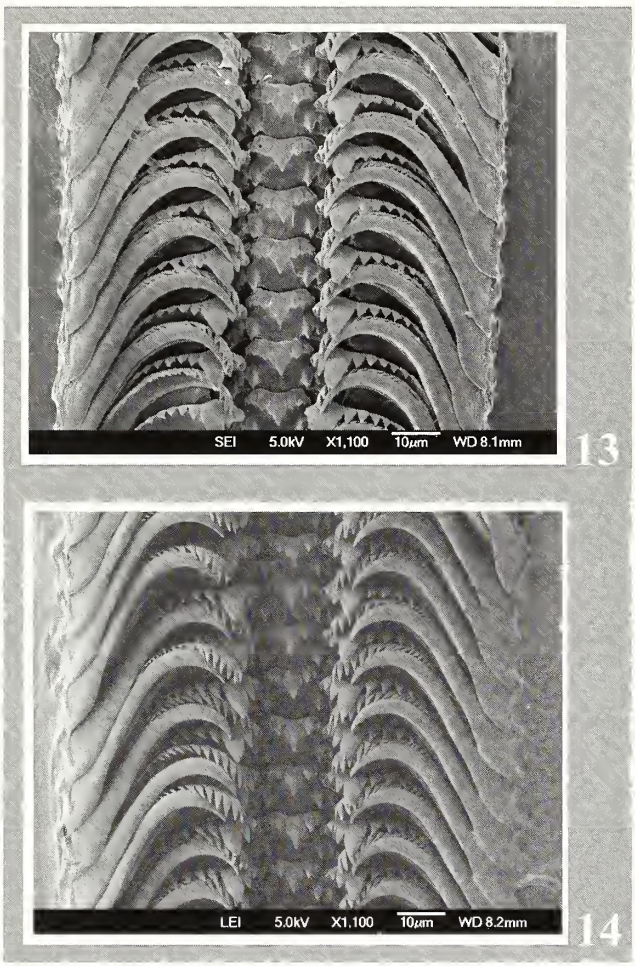
Figure 12. Thin plate spline representations for RW2, showing the deformation of the grid for the average values of *R. guerinii* (left) and *R. lia* (right).

erroneously classified specimens of *R. lia* were observed. In Figure 12 the thin plate spline representation allows interpretation in geometrie terms the positive (eharacteristic of *R. lia*) and negative deviations (characteristic of *R. guerinii*) values for the most signifieant non uniform shape variable, RW2, between the two species.

Radular Analysis: No relevant differenees emerged between the radulae of *R. guerinii* (Figure 13) and *R. lia* (Figure 14) in relation to the shape of teeth and cusps. Rachidian with one median eusp, two pairs of lateral cusps and two pairs of basal cusps. Lateral tooth with a median primary bigger cusp with respectively 2–3 inner cusps and 4–5 outer eusps in *R. guerinii* or 2 inner eusps and 3–5 outer cusps in *R. lia*. Figure 15 represents the frequeney distribution of the number of eusps of the lateral tooth observed in the sample studied and shows higher variability in *R. guerinii* for this charaeter.

Molecular Systematics: The topologies of the P and ML trees (Figure 16 and 17) were comparable: two main clades, corresponding to *R. guerinii* and *R. lia*, clearly separated from each other and from the outgroups by high bootstrap values.

Two individual sequences of *R. guerinii* formed a weakly supported clade elosely related to the main one of *R. guerinii*. The MJ network (Figure 18) showed two eonsistently distinct (18 differences) elusters of haplotypes (corresponding to *R. guerinii* and to *R. lia*). *R. guerinii* displayed higher genetic structure than *R. lia*, with one haplotype occurring in 29 specimens, 2 oecurring in 2 specimens and 11 unique haplotypes. No single haplotype of *R. lia* appeared to be dominant: the most common ones oeeurred in 11, 8, 5, 5 and 2 specimens; 3 were unique. Both clusters were consistently distant from 5 out of 6 outgroups, with *R. lia* closer than *R. guerinii*. Unexpectedly *R. auriscalpium* revealed very little difference (1–2) from some *R. guerinii* haplotypes.



Figures 13–14. SEM photographs or the radular ribbon of *R. guerinii* (13) and *R. lia* (14). Scale bar = 10 µm.

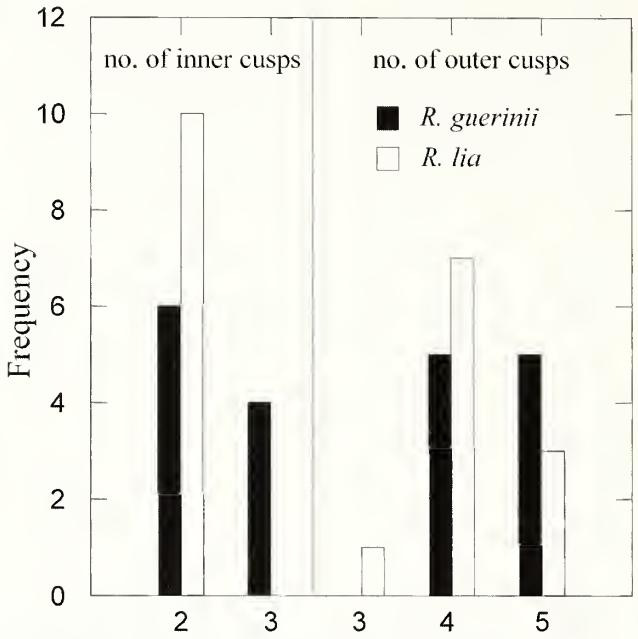


Figure 15. Frequency histograms of distribution of inner and outer cusps in the lateral tooth of *R. guerinii* and *R. lia*.

Dautzenberg Collection Material

Shell Visual Observations: *Rissoa guerinii*: The shells of the lot Rga were considerably worn, younger whorls in most uniformly whitish, in some uniformly yellowish; older 2–4 whorls always pale violet. Most of the shells of Rgb showed worn whitish/yellowish lowermost whorls and remaining whorls with the pigmentation described for *R. guerinii* typical. Shells of Rgc were better preserved and showed the chessboard (or zigzag) pattern described above for *R. guerinii* "var. *conspersa*".

Rissoa lia: Shells of Rlma and Rlmb were topotypes, the former being also from Monterosato collection. Although these shells were rather worn, the two colour varieties, described above for *R. lia*, were still detectable on the younger whorls but had completely disappeared from the whitish oldest whorls.

Shells of Rlp and Rlt were worn but a different pattern, with a whitish spiral band running in the middle of the youngest whorls on a dark brown background.

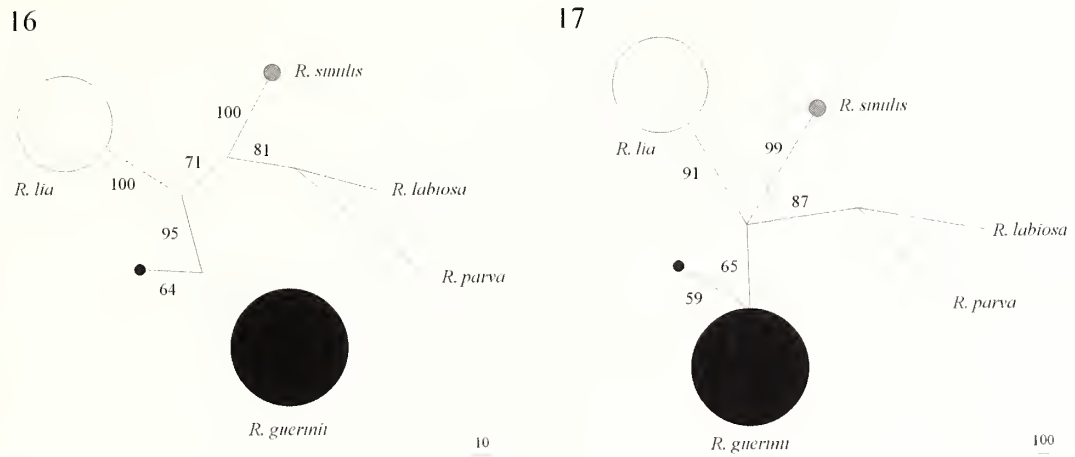
DISCUSSION

Shell and Head-foot: While in the early malacological literature satisfactory descriptions of the shell of *R. guerinii* are available (Jeffreys, 1869; Fretter and Graham, 1978), descriptive data on *R. lia* are limited to its essential original description (Monterosato, 1884; page 139).

Verduin (1985) provided a reinterpretation of the two taxa, stressing an extremely close morphological resemblance between them. However he based his diagnosis only on museum dry material, often in a poor state of preservation. As an example, the character "punctate spiral striae" (Verduin, 1985, pages 112 and 114), reported for the shells of both species, should be considered the result of the deterioration of the subtle reticulate pattern, formed by growth lines and spiral ridges and easily visible in fresh shells.

The redescriptions provided here are based on fresh shells at terminal growth, which maintain the peculiar characters of ornamentation and pigmentation of each species, but at the same time are readily matched with original museum material.

Dautzenberg and Durouchoux (1914), on the basc of the material of the lots here named Rga, Rgb, and Rgc, described four colour varieties for *R. guerinii*: typical (white with the intervals among ribs brown), *conspersa* (brown background with a chessboard pattern formed by very small spots), *albina* (totally white) and *bipartita* (with the first five or four whorls dark violet and the remaining entirely white). Based on the same material, Verduin (1985) even suggested the presence of a northern *R. guerinii* subspecies (showing the latter two color



Figures 16–17. Parsimony (16) and Maximum Likelihood (17) Trees drawn after the analysis of 16S sequences of *R. guerinii* and *R. lia*. Circle radius is proportional to sequences frequency. Bootstrap values are given at the left side of each branch.

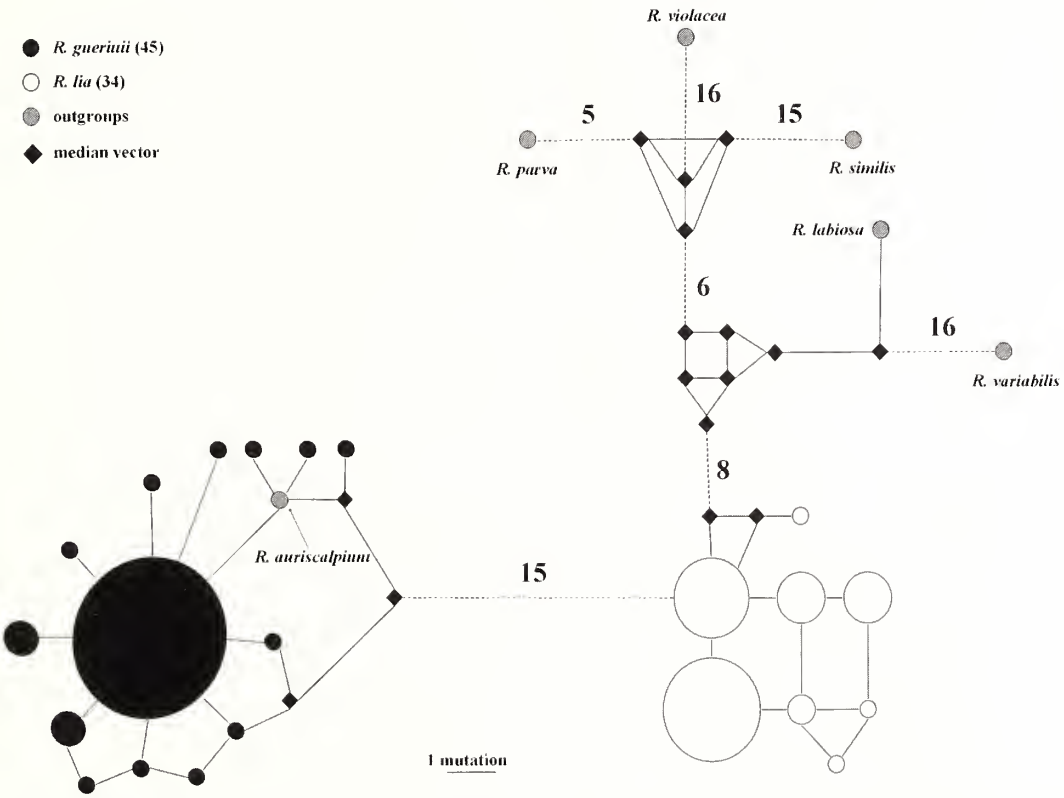


Figure 18. Median Joining Network drawn on the basis of 16S sequences. Number of sequences employed in brackets. Circles radius proportional to haplotype frequency. Dashed lines represent mutational distance higher than 4 (values reported nearby).

varieties) and a southern one (showing the former ones). We cannot see any justification for these claims as the varieties *albina* and *bipartita* are the result of the deterioration of the typical pigmentation, as shown by the worn shells forming the lots Rga and Rgb.

Although his interpretation of *R. lia* (based on the observation of Rlma and Rlmb lots) is generally correct, Verduin (1985: 114) added to its species diagnosis the observation that "in a sample from Trapani, Sicily (fig. 25) many colours and colour patterns can be discerned, among which the colour pattern *conspersa* known in *R. guerinii*."

This observation apparently suggested to Verduin (1985) the idea to move *R. lia* from the subgenus *Apicularia* Monterosato, 1884, to *Goniostoma* Villa, 1884 (the same subgenus of *R. guerinii*). We regard his observation as incorrect and in disagreement with the original description of Monterosato (1884) and with our observations on the material in this study. We found no evidence

that the color pattern *conspersa* belongs to *R. lia*. Although we could not examine the sample mentioned by Verduin (1985), an examination of the figures he provided (25a–h), allowed us to assess that these figures are composed by a mixture of shells of *R. lia* and *R. guerinii* shells, associated because of their similar apex dimensions.

However, the statement that some *R. lia* show "the presence of broken brownish colour lines which encircle the shells" (Verduin, 1985: 114), is in agreement with observations made on lots Rlp and Rlt and with some recent peculiar records of *Rissoa* sp. from Sardinia (Tyrrhenian Sea), showing this same peculiar coloration (Fasulo, pers. comm.). Although this coloration is not typical of the type material of *R. lia*, further observation on live-collected material from these localities is needed to properly address the issue.

Rissoa species tend to maintain the head-foot colour pattern (i.e., position and dimensions of elements as spots or blotches), although they may show intraspecific variation in colour intensity (Fretter and Graham, 1978). This phenomenon has been employed to support species identity (*R. parva* and *R. interrupta*, Warén, 1996; *R. guerinii* and *R. panlormensis*, Criscione et al., 2009) or to hypothesize recent speciation (*R. membranacea* type A and B, Rehfeldt, 1968; *R. auriscalpium* type a and b, Colognola et al., 1986). This rule is in agreement with the slight variation in color intensity observed in this study for the two varieties of *R. guerinii*, but it does not apply to *R. lia*, whose color varieties showed two distinct patterns.

Traditional Morphometry: Although the present morphometric analysis is restricted to populations from a single locality, its results are not only helpful in understanding intrapopulation variability in shell morphology, but also in drawing more general conclusions in terms of specific differentiation. The differences observed can be expressed in terms of teleoconch and protoconch variation, with the first element being by far the most important. Populations of both species show a wide variability in protoconch dimensions, which is larger for *R. guerinii*. *Rissoa lia* shows twice the intrapopulation variation in teleoconch characters than that observed for *R. guerinii*.

The values of shell parameters obtained for the two species showed a considerable overlap, which is mainly dependent on the strong similarity in protoconch dimensions and not, surprisingly, by the resemblance of the teleoconchs. Most shells of *R. guerinii* appear to have a larger relative size, a more elongated aperture and to be more slender than most *R. lia* shells.

Discriminant analysis showed that *R. guerinii* and *R. lia* populations can be distinguished mainly for the more elongated aperture of *R. guerinii* shells, for their larger relative size, and the higher slenderness. The importance of protoconch is only marginal.

In summary, our results show that teleoconch morphometry can be efficiently used to discriminate between *R. guerinii* and *R. lia*, whereas protoconch dimensions are less representative of the overall interspecific variation and less reliable, due to the large overlap shown. This idea is in contrast with the view of the discriminating power of protoconch dimensions (Verduin, 1986).

Some Methodological Considerations: Cadèe (1998: 91) critically revised the methodology used by Verduin (1976, 1982b, 1985, 1986) highlighting that the measurements of d and D_0 "depend on the accurate vertical position of the shell and the somewhat arbitrary location of the line along which d and D_0 are measured." Cadèe (1998) dealt with the former issue by performing repeated measurements of d and D_0 on specimens of *R. membranacea*, whose vertical placement was reiterated ten times, and obtained a standard deviation of about 0.01 mm for both the variables. This value is roughly the same as that which separates the mean values of d and D_0 of *R. lia* and *R. guerinii* in this study (not shown). This means that some of the differences in protoconch dimensions might be indeed the consequence of the inaccurate measurements, rather than representing real variation. The alternative solution of performing measurements on digital photographs has been also recently employed (Criscione et al., 2009). The second issue is that real *Rissoa* protoconchs often do not correspond to the ideal shell apex figured by Verduin (1977; Figure 1), but most of them are rather irregular. In protoconchs like these there is a large range of possibilities to locate the line along which d and D_0 should be measured and the choice is largely arbitrary.

Geometric Morphometry: The ANOVA revealed a significant larger size (CS) of the shells of *R. guerinii* compared to those of R. *lia*, confirming the results of visual observations and traditional morphometry. ANOVA showed a significant difference ($p<0.05$) between the two groups in the first (RW1) and the second (RW2) non-uniform shape variables. The significance for RW2 remained unaltered when correcting the analysis for CS (ANCOVA), while that of RW1 was not significant, indicating that the shape difference explained by that variable was dependent on size. This means that the two groups differ exclusively on the second non-uniform shape variable (RW2), independently from the correlation between shape and size.

The discriminant function calculated from all the non-uniform shape variables, was successful in morphometrically discriminating the two groups. RW2 was the most important variable in determining the distinction between *R. guerinii* and *R. lia*. The mean values of this variable for each of the two groups (positive for *R. lia* and negative for *R. guerinii*) were plotted in a tps representation (Figure 12). The plot showed that that variable RW2 is a reflection of the most obvious discernable shell shape difference. This comprised the more fusiform shape of R. *guerinii*, contributed by consistently narrower whorls than those of *R. lia* (represented by the contraction of the corresponding zone of the grid) and a substantially equal penultimate whorl.

The grid deformation in the plot of *R. lia* increase progressively from the top to the middle-lower as expected for a more conical shape. In the same plot, larger deformations of the upper part and the lower of the grid for *R. lia*, account respectively for the more obtuse apex and the larger aperture of *R. lia*.

Radular Analyses: Although the taxonomical value of radular morphology in rissoids is exclusively limited to generic level (Ponder, 1985), comparative analysis of patterns of similarity may be helpful in resolving the complexity of a highly diverse genus such as *Rissoa*. Along with other characters, differences in the size of the cusps of marginal tooth have been employed to show differences between two morphs of *R. auriscalpium* (Colognola et al., 1986) and radular identity has been used to support findings of recent speciation in *R. membranacea* morphs (Rehfeldt, 1968).

However, detailed reports on the taxonomic value of cusps in rissoids are lacking and this makes it difficult to give the appropriate weight to the difference between *R. guerinii* and *R. lia* in the relative number of cusps of the lateral tooth. But the pattern emerged appears to be rather constant and its eventual value as distinctive character of phylogenetic significance cannot be excluded.

Molecular Systematics: Analysis of mitochondrial sequences of gastropod taxa, involved in a recent speciation event (or an ongoing speciation process), often show traces of introgression (e.g., Kirby et al., 1997; Kojima et al., 2001). Introgression shown by 16S sequences has been used to support ongoing speciation in the P/NP pair of sympatric siblings *Rissoa auriscalpium/R. italiensis* (Panico and Patti, 2005). In this study, no evidence of introgression was detected for sympatric populations of *R. guerinii* and *R. lia*, suggesting that claims of recent speciation are not acceptable. However, the evolutionary rate of 16S rRNA is not known in rissoids and the hypothesis of an earlier cladogenetic event, giving rise to *R. guerinii* and *R. lia*, cannot be excluded. The results of our molecular analysis also challenge the likelihood of this scenario.

The ML analysis (Figure 17) failed in resolving the polytomy resulted for sequences of *R. guerinii*, *R. lia* and one of the outgroups, *R. similis*, as expected if our ingroups were sister species. Before Verduin (1985) moved *R. lia* to the subgenus *Goniostoma*, a closer relationship between this species and *R. similis* was commonly accepted (as both members of the subgenus *Apicularia*). Our results may be considered in agreement with this idea.

The hypothesis of the shared origin of *R. guerinii* and *R. lia* would require much lower mutational distance between the two sister species than between each sister species and the outgroups. Our MJ network (Figure 18) shows that this is not the case. *R. lia* is separated from the main haplotype of *R. guerinii* by a distance of the same order of magnitude than the distance separating this species from the other outgroups.

The significant difference in haplotype diversity of *R. guerinii* and *R. lia* (shown by the same analysis) may be the result of stochastic events in the evolutionary history of these lineages or may be alternatively related to the supposed alternative strategy of larval dispersal (P/NP). *Rissoa guerinii* displays a higher genetic structure which may reflect a higher genetic flow, due to its higher dispersal capability. Conversely, *R. lia* shows a lower structure which would reflect a lower level of gene flow. Despite records of *R. guerinii* planktotrophic veligers have been long reported (Lebour, 1934; Thiriot-Quievreux and Babio, 1975), no evidence for the non-planktotrophic strategy of *R. lia* are known and successful laboratory experiments on spawning are lacking. The actual strategy of dispersal of the two species is thus still to be confirmed.

Surprisingly, an outgroup sequence of *R. auriscalpium* showed only two differences from the main *R. guerinii* haplotype. This short distance fits in the normal intraspecific (and even intrapopulational) variability of *R. guerinii* and represent a clue of previously unsuspected genetic similarity between the two species. Further investigation is required to properly address the issue.

CONCLUSIONS

The taxonomic revisions of Verduin (1976, 1977, 1982b, 1985, 1986), although based exclusively on empty shells, have represented landmarks in the α-taxonomy of *Rissoa*. Despite some evidence of the taxonomic unreliability of shell characters in *Rissoa* (*e.g.*Wigham, 1975; Warén, 1996), only a few attempts have been made to dispute his conclusions. These include criticism of his methods (Cadée, 1998) and the utilization of non shell-based approaches (Colognola *et al.*, 1986; Panico and Patti, 2005; Criscione et al., 2009). This trend has been followed in our work, which demonstrates the value of a synergy between modern techniques applied to the analysis of shell characters and molecular methods. The present study has shown that the very similar shell morphology of *R. guerinii* and *R. lia* hides a clear distinction in other characters, indicating that they should not be considered as a cryptic pair of sister taxa.

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We are grateful to Dr. Danilo Scuderi (Università di Catania) for having provided the drawings shown in Figures 6–9. We would also like to thank Prof. Jackie Van Goethem and Prof. Thierry Backeljau (RBINS) for the possibility to study Dautzenberg collection material. We want to express gratitude to Prof. Domenico Caruso and Prof. Grazia Cantone (Università di Catania) for financial support, the Molecular Biology Service and the Scanning Electron Microscopy Service of Stazione Zoologica "Anton Dohrn" (Naples). We are also thankful to Dr. Winston F. Ponder and an anonymous referee for their valuable comments.

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Molecular phylogeny of *Conus chiangi* (Azuma, 1972) (Gastropoda: Conidae)

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ABSTRACT

Conus chiangi (Azuma, 1972) has been regarded by several workers as morphologically distinctive enough from other *Conus* species to merit placement in its own genus (e.g., *Taranteconus*, Azuma, 1972). We demonstrate using standard molecular markers that this species is related to such well-known species as *Conus imperialis* Linne, 1758, and *Conus regins* Gmelin, 1791, which are generally regarded as belonging to the *Stephanoconus* (Mörch, 1852), clade. *Stephanoconus* has had impressive radiation of species in the new world, but only two species were previously assigned to *Stephanoconus* from the Indo-Pacific region (*Conus imperialis* and *Conus zonatus* Hwass, 1792).

We also present data using a toxinological marker for *Conus chiangi* consistent with its inclusion in *Stephanoconus*. In at least three species of this clade, a virtually identical peptide toxin (first called α-conotoxin ImI from *Conus imperialis*) was identified. Although the predicted mature peptide toxin sequences are closely similar, significant divergence in the prepro region of the precursors was observed. It is suggested that the conservation of the mature peptide toxin sequence is a result of strong selection related to prey choice in *Stephanoconus*.

The results described here suggest a revised picture of the radiation of *Stephanoconus* in the Indo-Pacific. In addition to the well-known species *Conus imperialis* and *Conus zonatus*, which comprise one group, a radiation of small *Conus* species in deeper water may potentially comprise another distinctive group of *Stephanoconus*.

Additional keywords: Conotoxins, peptides, DNA sequence, molecular markers

INTRODUCTION

Conus chiangi (Azuma, 1972), is a morphologically unusual *Conus* species that differs strikingly from other *Conus* in its spire sculpture (see Figure 1). For many years, *Conus chiangi* was extremely rare and, only very occasionally collected. The type locality is in the South China Sea; a junior synonym of *Conus chiangi* is *Conus lamellatus* (Suzuki, 1972) — the type of *Conus lamellatus* was collected off of Sumisu Island, near Hachijo Island, Izu Peninsula, Japan. Probably because of the unique scale-like spines that line the shoulder margins of the spire, both Azuma and Suzuki proposed that this species defined a new genus: Azuma designated *Taranteconus* as a new genus for this species while Suzuki proposed *Cornutoconus*, reflecting the perceived uniqueness of *Conus chiangi*. The taxonomy of *C. chiangi* has been discussed by Coomans et al. (1983) and Röckel et al. (1995).

More recently, a number of specimens of this unusual cone snail have been collected in the Philippines. Initially, collectors using tangle nets obtained specimens from Cebu and around Bohol Islands. Then, more recently, use of small trawls allowed for collection of an even larger number of specimens off Aliguay Island. Philippine specimens are shown in Figure 1, including an inset illustrating the characteristic spire structure. In this work, we describe a molecular analysis of *Conus chiangi*, using a number of different genetic markers to provide insights into the relationship of *Conus chiangi* to other species of *Conus*. Additionally, we present some unexpected results illustrating selection for conservation of a toxin expressed in *Conus chiangi* venom ducts.

In combination, the data we present below demonstrate that *Conus chiangi* is not phylogenetically distant from other *Conus* species. Thus, there is no justification for the erection of a new genus for this species, given that *Conus chiangi* is shown to be closely related to well-known species such as *Conus imperialis* Linne, 1758, and *Conus regius* Gmelin, 1791, which belong in the *Stephanoconus* clade. This conclusion is reached consistently, no matter which genetic locus we used for the phylogenetic analysis. The more general biological/evolutionary implications of these results are discussed.

MATERIALS AND METHODS

Preparation of Genomic DNA: Genomic DNA was prepared from 20 mg *Conus chiangi* hepatopancreas tissue using the Gentra PUREGENE DNA Isolation Kit Kit (Gentra Systems, Minneapolis, MN) according to the manufacturer's standard protocol.

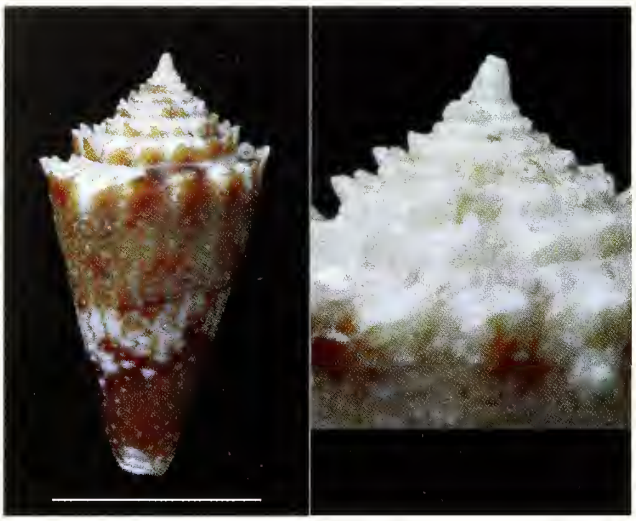

Figure 1. *Conus chiangi* (Azuma, 1972). Left: A specimen of *Conus chiangi*, collected off Aliguay Island, Philippines. Right: The spire of a different specimen of *Conus chiangi*, showing a close-up of the unusual scale-like spine morphology of the spire shoulder margins. Scale bar = 1 cm.

Cloning and Sequencing of 12S and 16 mitochondrial RNA segements and Cytochrome Oxidase subunit I mitochondrial RNA gene segment (BarCOI)

Ten ng of *Conus chiangi* genomic DNA was used as a template for polymerase chain reaction (PCR) with oligonucleotides eorresponding to 12S-I (5′ TCG CAG CAG YCG CGG TTA) and 12S-III (5′ AGA GYG RCG GGC GAT GTG T) mitochondrial rRNA segments and 16SH (5′ CCG GTC TGA ACT CAG ATC ACG T) and 16LC (5′ GTT TAC CAA AAA CAT GGC TTC) mitoehondrial rRNA segments, and oligonueleotides corresponding to COI dgl CO-1490 (5′ GGT CAA CAA ATC ATA AAG AYA TGY G 3′) and COI dgHCO-2198 gene segments (5′ TAA ACT TCA GGG TGA CCA AAR AAY CA 3′). The per cycling profiles are as follows: Initial denaturation (95°C, 60 s); followed by 40 eycles of denaturation (95°C, 20 s); annealing (55°C, 20 s) and extension (72°C, 30 s). The resulting PCR products were purified by gel electropheresis, recovered from agarose using High Pure PCR Product Purifieation Kit (Roehe Diagnostics, Indianapolis, IN). The eluted DNA fragments were annealed to pNEB206A vector using the USER Friendly Cloning kit (New England BioLabs, Inc., Beverly, MA) following manufacturer's suggested protocol and the resulting product transformed into DH5a competent cells. The nucleic aeid sequences of the resulting 12S, 16S and COI-encoding clones were determined according to the standard protocol for Automated sequencing.

Phylogenetic Analysis: Sequences which were first aligned with Clustal X (Larkin et al., 2007) and then refined by eye align obviously homologous regions that Clustal failed to recognize. Individual genes were eoneatenated with MaeClade 4.08 (Maddison and Maddison, 2005).

Sinee MrBayes (Huelsenbeck et al., 2001) has the eapability to eompletely stratify maximum likelihood model parameters by gene and by codon position (Ronquist and Huelsenbeck, 2003), we ehose it as the primary method of tree eonstruetion. Eaeh analysis comprised two simultaneous runs with four chains each. All runs were suffieiently long to minimize the average standard deviation of the split frequeneies (below 0.05 for COI and 0.007 for 12S rRNA and for the eoneatenated sequence of 3 genes. Plots of the number of generations against the maximum likelihood scores indicated apparent equilibrium. Further diagnostics ineluded the potential seale reduction factor (PSRF) that measures the fit of branch length and all parameters. Trees and parameters from the first 25% of the generations were disearded (the burn in) after completion of the MCMC (Monte Carlo Markov Chain) seareh. Bayesian analyses eomprised two runs with four ehains each.

We also used maximum likelihood analysis using models optimized in PHYML (Guindon and Gascuel, 2003). For each tree, we ran a heuristie maximum likelihood seareh followed by analysis of 1000 bootstrap replieates to plaee eonfidenee limits on the trees.

Identification and Sequencing of clones encoding Ch1.I

Genomie DNA from *Conus chiangi*, prepared as deseribed above, was used as a template for polymerase ehain reaction (PCR) with oligonucleotides corresponding to the eonserved intron and 3′ UTR sequences of previously isolated α-eonotoxin genes:

Forward primer: 5′ TGT GTG TGT GTG GTT CTG GGT 3′

Reverse primer: 5′ CTC GAG GTC GTG GTT CAG AGG 3′

The PCR eyeling profiles are as follows: Initial denaturation (95°C, 60 s); followed by 40 eyeles of denaturation (95°C, 20 s); annealing (62°C, 20 s) and extension (72°C, 30 s). The resulting per products were purified using the High Pure PCR Produet Purifieation Kit (Roche Diagnosties, Indianapolis, IN) following the manufaeturer's suggested protocol. The eluted DNA fragments were annealed to pNEB206A veetor, and sequenced as described above.

RESULTS

Molecular phylogeny of *Conus chiangi*: In order to assess the phylogenetie relationships of *Conus chiangi* to other *Conus* species, the sequenees of three standard molecular markers were obtained as described under Materials and Methods above: COI, 12S, and 16S. A tree based on the COI sequences is shown in Figure 2; a set of COI sequences from a much larger number of *Conus* species were initially analyzed. Only a small subset of these results is shown, including the speeies found to be most elosely related to *Conus chiangi*. The data

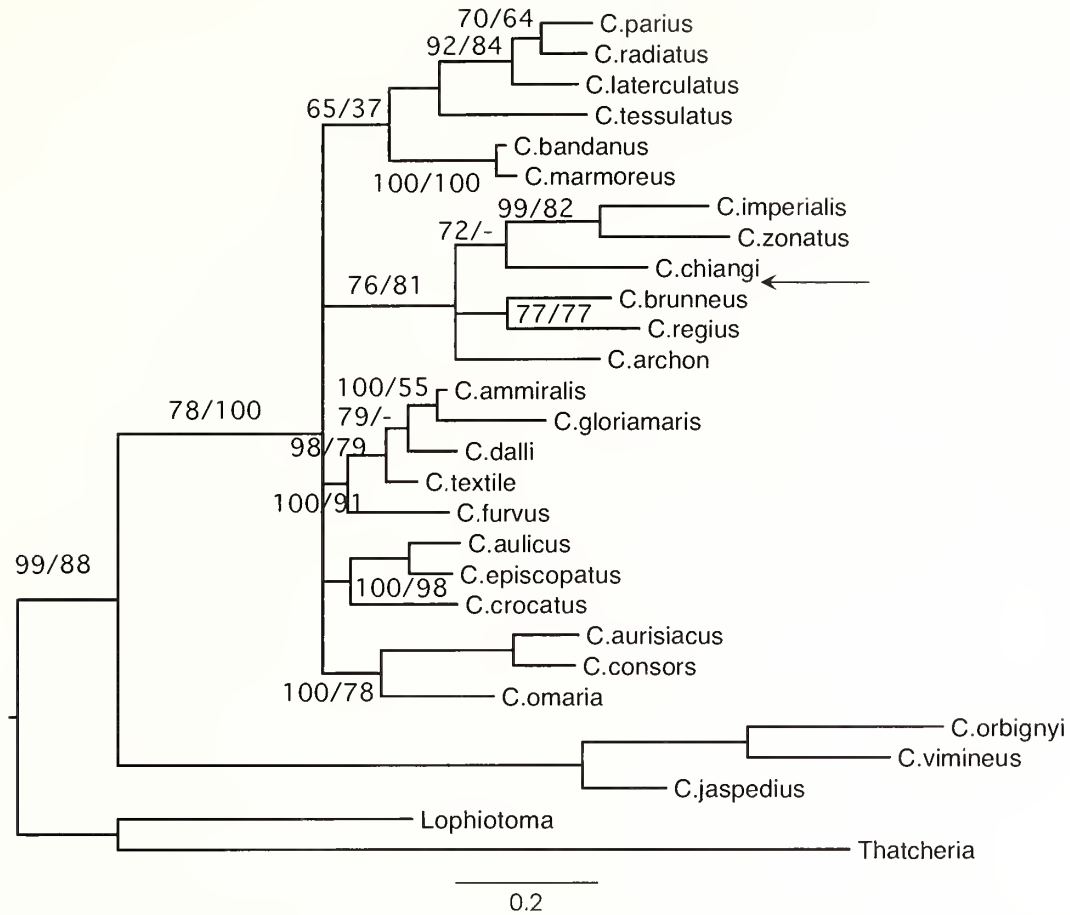

Figure 2. A Bayesian phylogenetic tree based on COI sequences. Numbers to the left of the slash are Bayesian posterior probabilities expressed as percentages. Numbers to the right are maximum likelihood bootstrap percentages. Dashes or blanks mark support values less than 50%. These data suggest that *Conus chiangi* is related to *Conus imperialis* and *Conus zonatus*. Sequences of the COI marker of a much larger number of *Conus* species have been obtained, but only a few clades are shown.

presented in Figure 2 suggest that *Conus chiangi* is related to two shallow-water Indo-Pacific species, *Conus imperialis* and *Conus zonatus*. These two species belong to a clade known as *Stephanoconus*, which comprises cone snails known to specialize on devouring amphinomid polychaetes ("fireworms"). There is a greater biodiversity of this group in the new world; in the Indo-Pacific, the only species that are generally assigned to the *Stephanoconus* clade are *Conus imperialis* and *Conus zonatus* (Duda Jr et al., 2001; Espiritu et al., 2001).

The position of *Conus chiangi* was independently assessed using 12SrRNA sequences (Figure 3). These data strongly indicate that *Conus chiangi* is a member of the *Stephanoconus* clade.

We found that an alignment of 16SrRNA, by itself, had too little phylogenetic signal to yield a meaningful tree. However, combining the gene with 12S and COI in a stratified analysis increased the phylogenetic signal to the extent that the relationship of *C. chiangi* with the other *Stephanoconus* species became clear (Figure 4). In this case, there is a 100% posterior probability that *Conus chiangi* belongs within the *Stephanoconus* clade with *Conus regius* and *Conus imperialis*. Furthermore, the data suggests that there are three groups in the clade, one that includes the large Indo-Pacific forms (*Conus imperialis* and *Conus zonatus*), one that includes some of the new world forms (*Conus regius* Gmelin, 1791, and *Conus brunneus* Wood, 1828) and *Conus chiangi*, which in this phylogeny somewhat surprisingly groups together with the Panamic species *Conus archon* Broderip, 1833.

Toxinology: The discovery that *Conus chiangi* venom ducts expressed a certain type of venom peptide (i.e., α-conotoxins (Santos et al., 2004) belonging to the α4/3 subfamily) was an early indication that the species might be a member of the *Stephanoconus* clade (Ellison et al., 2008). Only species in the *Stephanoconus* clade are known to express this unusual group of *Conus* venom peptides, which are targeted to nicotinic acetylcholine receptors. We report here an even more striking

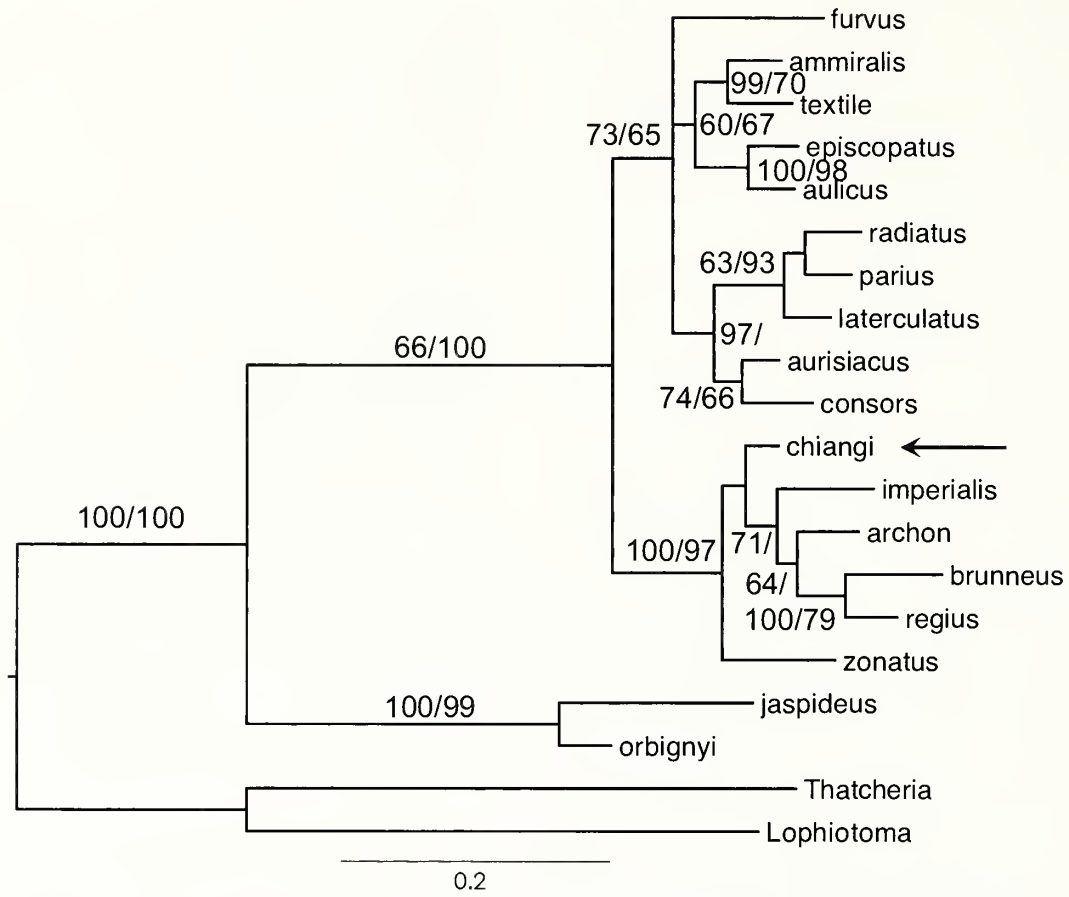

Figure 3. 12SrRNA tree inferred from Bayesian analysis. A topologically identical tree was inferred using maximum likelihood analysis. Branch labels are as described in Fig 2. Note that the clade defined by the bold line (*Stephanoconus*) is well supported using this molecular marker.

illustration of the close affinity of *Conus chiangi* to other species in the *Stephanoconus* clade.

An analysis of peptides in the venom ducts expressed in *Conus chiangi* has revealed a precursor to a peptide previously extensively characterized, α-conotoxin ImI from *Conus imperialis* (McIntosh et al., 1994). In general, there is a striking sequence divergence between *Conus* peptides from different species. The discovery that a peptide identical to α-conotoxin ImI is expressed in the venom duct of *Conus chiangi* provides additional support that the two species are related.

A comparison of precursor sequences predicted from clones obtained from *Conus chiangi, Conus imperialis* and *Conus regius* is shown in Figure 5. The sequences are aligned to maximize sequence identity. Because the predicted precursor sequences for *Conus imperialis* and *Conus regius* were obtained from a genomic clone (see Materials and Methods), these precursor sequences were incomplete but the available sequences have been aligned. The predicted mature peptides are shown in the figure, with the predicted cleavage signals for proteolytic processing underlined.

The sequences shown in the figure reveal that although the mature peptides from *Conus imperialis* and *Conus chiangi* are identical (and the mature peptide from *Conus regius* almost identical); the inferred precursor sequences indicate considerable divergence in the propeptide region. Thus, this is an unprecedented example of identical or almost identical mature peptide sequences with significant differences in the propeptide region of the precursor. The potential significance of these data will be discussed below. However, these results are strong evidence for the close relationship between, and potentially similar biology of, *Conus chiangi, Conus imperalis* and *Conus regius*.

DISCUSSION

The data presented above were obtained from two types of experimental approaches. The phylogentic relationship of *Conus chiangi* to other *Conus* species was first evaluated using three standard marker genes. *Conus chiangi* appears well embedded within the major clade of cone snails (Bandyopadhyay et al., 2008; Puillandre

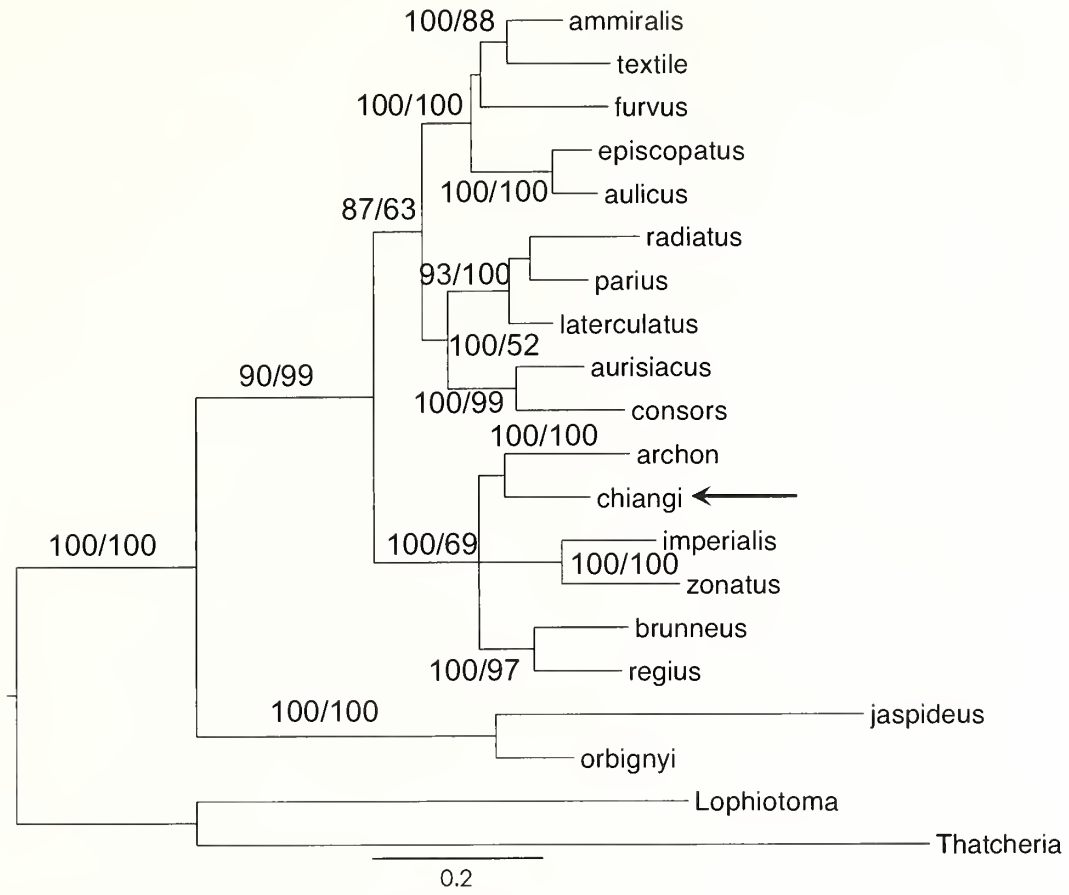

Figure 4. A phylogenetic tree combining all three molecular markers obtained, COI, 12S and 16S) in a stratified Bayesian analysis. An identical maximum likehood tree supports this topology. Labels are as in Figure 2. In this case, the assignment of *Conus chiangi* to the *Stephanoconus* clade (type of the proposed subgenus *Stephanoconus* is *Conus regius*) is well supported.

Sequences from genomic clones:

Ch1.1	...FDGRNAAADDKASDLIAQIVRRGCCSDPRCAWRC
α-ImI	...LEERNAPADDKASDLIAQIVRRGCCSDPRCAWRC
Rg1.9	...FNGRSAAADQNAPGLIAQVVRGGCCSDPRCAWRC

Predicted mature α-conotoxin sequence:

Clone	Species	Predicted toxin sequence
Ch 1.1	*Conus chiangi*	GCCSPDRCAWRC#
αImI	*Conus imperialis*	GCCSPDRCAWRC#
Rg1.9	*Conus regius*	GGCCSPDRCAWRC#

Figure 5. Similarity of mature α-conotoxin sequences of *Conus chiangi* with those from *Conus imperialis* and *Conus regius*. Shown are data obtained from genomic clones from *Conus chiangi*, *Conus imperialis* and *Conus regius*. The predicted proteolytic processing site following which cleavage occurs to release the mature toxin is underlined. Note that the mature toxin sequences are virtually identical in the three species despite considerable divergence in the propeptide region. # - denotes an amidated C-terminus

et al., 2008) and is most closely related to *Conus* species traditionally assigned to the *Stephanoconus* clade.

The second type of data described above were toxinological markers; these are also consistent with the assignment of *Conus chiangi* to the *Stephanoconus* clade. The discovery of identical or almost identical peptide sequences from the venom ducts of *Conus chiangi*, *Conus imperialis* and *Conus regius* establishes the close relationship between the three species despite the strikingly divergent shell morphology of *Conus chiangi*. In contrast to the other two shallow-water species, it is only found in relatively deep water (200–300 meters). This is the first documentation of almost identical peptides from three different *Conus* species—even peptides that seem to share the same molecular targeting specificity can vary greatly in their primary amino acid sequence if closely related *Conus* species are compared. α-Conotoxin ImI has been an extensively characterized competitive antagonist of nicotinic acetylcholine receptors. In the mammalian nervous system, this peptide competitively antagonizes a

Figure 6. Shells of some species in the *Stephanoconus* elade. All speeies in the *Stephanoconus* clade that are ineluded in the analysis in Figure 4 are shown. Top, left to right: *Conus chiangi, C. imperialis, C. zonatus;* bottom, left to right: *C. regius, C. archon, C. brunneus*. The specimen of *Conus brunneus* shown is a juvenile (when adult, it is approximately the same size as the specimen of *Conus regius*). All of the other specimens, ineluding *C. chiangi* are full-sized adults. Note how mueh smaller *Conus chiangi* is than the other species in this clade. Scale bar = 1 cm, applies to all images.

variety of neuronal subtypes, including α7 and α3β2 nicotinic receptors. Injection of the peptide into the central nervous system of a mouse elieits partial seizures.

Potentially more relevant to the biology of the eone snails is the observation that this peptide also inhibits one of the nicotinic acetylcholine receptors at the neuromuscular junetion of the nematode *Caenorhabditis*

elegans (J. Richmond and E. Jorgensen, unpublished results). Thus, the peptide appears to be active over a broad phylogenetic range, although it seems to be highly selective for a specific subset of nicotinic acetylcholine receptors in an individual nervous system. In invertebrates, it may well be targeted to nicotinic receptors that are important for neuromuscular transmission, and thus may be a major venom component that enables polychaete-hunting cone snails to cause prey paralysis.

The unusual conservation of the mature toxin region may be a consequence of the small size of this peptide. There may be stringent selection on the sequence of the peptide. There is some direct evidence to support this: native peptides that are closely homologous in sequence, such as α-conotoxin ImII and α-conotoxin RgIA, have different molecular targeting specificity (for a review, see Olivera et al., 2008). Thus, the mature α-conotoxin ImI peptide, which is also found in *Conus ehiangi* venom, has presumably been optimized by strong selection, and given the small size, does not show the typical hypervariability that can be demonstrated in larger homologous peptides from different *Conus*. Nevertheless, that the genes involved are subject to hypervariation is demonstrated by the lack of conservation in the propeptide region between the three species compared in Figure 5.

Thus, despite highly divergent morphological characteristics of the shell of *Conus ehiangi*, it is clearly related to other *Conus* and there would appear to be no justification for separating it into a separate genus. The assignment of *Conus chiangi* to the genus *Conus* (and subgenus *Stephanoconus*) would be consistent with the results presented above. [It should be noted that some workers (see for example da Motta, 1991) do not assign *C. imperialis* to *Stephanoconus*, but to *Lithoconus* Morch, 1852. Since the type of *Lithoconus* is *C. leopardus*, which is not closely related to *C. imperialis* by molecular phylogeny, the assignment to *Stephanoconus* seems more appropriate].

A curious feature of the *Stephanoconus* clade (see Figure 6 for some examples) is that there were relatively few species assigned to this clade in the Indo-Pacific, with greater biodiversity in the Caribbean/Eastern Pacific. Although not all candidates for assignment to the *Stephanoconus* clade have been directly analyzed using molecular markers, it seems likely that *Conus brunneus* Wood, 1828, *Conus bartschi* Hanna and Strong, 1949, and *Conus archon* Broderip, 1833, in the Eastern Pacific, and *Conus regius* Gmelin, 1791, *Conus aurantius* Hwass, 1792, and the complex of forms related to *Conus cedonulli* Linne, 1767 in the Caribbean, are members of the *Stephanoconus* clade. Although the Indo-Pacific has much greater biodiversity of *Conus* species in general, only two species have routinely been assigned to this clade, the widely distributed *Conus imperialis* Linne, 1758, and *Conus zonatus* Hwass, 1792, found in the Indian Ocean from South India to Western Thailand. The results of our study, which has revealed that *Conus ehiangi* is well embedded in the *Stephanoconus* clade, raises the possibility that there is a deep-water Indo-Pacific radiation of *Stephanoconus*. It would seem useful to investigate whether other *Conus* species with unusual spire structures belong to this group, including two other small deep-water species, *Conus suidurati* and *Conus polongimarumai* Kosuge, 1980 (see Figure 7). From similarities in shell morphology, the latter seems particularly likely to be a deep-water *Stephanoconus* like *Conus ehiangi*.

The discovery that *Conus ehiangi* belongs to the *Stephanoconus* clade has biological implications: all

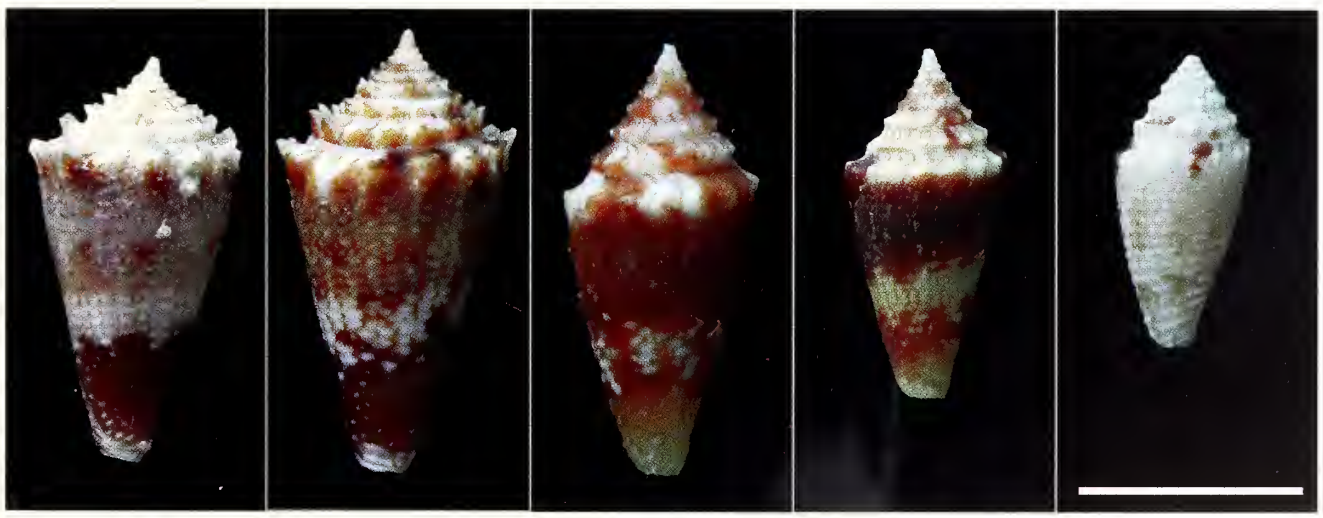

Figure 7. *Conus chiangi* compared to other putative members of a deep-water *Stephanoconus* clade. The two left-most specimens are *Conus chiangi*; the two middle specimens are *Conus polongimarumai* and the right-most specimen is *Conus suidirati*. The two species *Conus polongimarumai* and *Conus suidirati* are rare, and no molecular data has been obtained. Based on morphological criteria, these are candidates for inclusion in a deep-water Indo-Pacific clade of *Stephanoconus*, defined by *Conus chiangi*. Scale bar = 1 cm, applies to all images.

known members of the *Stephanoconus* clade whose prey preference has been defined eat amphinomid polychaetes ("fireworms") (Kohn, 1959; Röckel et al., 1995). The molecular phylogeny of *Conus chiangi*, and the conservation of venom peptides documented above, suggest that the prey preference of the species is related: likely small, deep-water amphinomids. Whether or not this prediction is true can be verified by a type of reverse ecological approach that was recently used for identifying the prey of some turrid species (M. Astilla and G. Concepcion, unpublished) in which a PCR analysis of the gut contents of several Turrid species (to identify the barcode sequence of recently ingested prey) was used. However, the tree in Figure 4 suggests that the deep water Indo-Pacific *Stephanoconus* diverged from the two shallow water species relatively early in the adaptive radiation of the clade, comparable in time to when the new world and old world branches diverged.

The *Stephanoconus* clade, as redefined here, has several intriguing features. It is one of the few worldwide clades within the genus *Conus*. In contrast to *Stephanoconus*, the *Conus* species that prey on fish display an entirely different biogeographic pattern. The available molecular data indicate that the new world piscivorous species evolved fish-hunting completely independently, and are not genetically more closely related to fish-hunting than to non fish-hunting *Conus* clades (Duda Jr. and Palumbi, 2004; Espiritu et al., 2001; Imperial et al., 2007) (Krause et. al., manuscript in preparation). The fact that *Stephanoconus* is both worldwide in its distribution, and significantly more species-rich in the new world, is different from most other characterized branches of *Conus*, suggesting an unusual evolutionary history of this group compared to other cone snail clades.

ACKNOWLEDGMENTS

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Testability of the Energy Maximization Model (Kitchell et al., 1981) of naticid predation on two bivalve prey from the eastern coast of India

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ABSTRACT

In 1981, Kitchell et al. envisaged a net energy maximization model that can rank different prey according to their preferences. Several workers tested the model both in experimental studies and in fossil records. In the present endeavor we have tried to analyze the nature, from a cost-benefit perspective, of naticid predation on two Recent prey bivalve species *Mactra luzonica* Reeve, 1854, and *Donax scortum* Linnaeus, 1758, collected from eastern coast of India. The results have broadly supported the theoretical cost-benefit curve of Kitchell et al. (1981). While *Mactra luzonica* was thoroughly preyed upon regardless of body size, predation on *Donax scortum* significantly decreased after prey body size exceeds 3 cm. This is explained on the basis of a change in mode of living of the prey during late ontogeny. Other factors like prey availability, prey ornamentation, consumption rate, and presence of secondary predators that may constrain the model, have been discussed.

Additional Keywords: Naticid predator, Indian coast

INTRODUCTION

Dynamics of predator-prey interaction have been a major subject of interest in current research (Reyment, 1966; Carriker, 1969; Kitchell et al., 1981; Vermeij, 1983; Anderson et al., 1991; Anderson, 1992; Tull and Böhning-Gaese, 1993; Kelley and Hansen, 1996; 2003; Dietl and Herbert, 2005, and references therein). Predation is the main driving force for change in community structure and coevolution of species (Vermeij, 1983; Boucher, 1988; Endler, 1991) within an environment.

Bivalves are mostly preyed upon by carnivore gastropods. Many of them make a characteristic borehole on the shell of prey either by mechanical rasping (Fischer, 1922; Pelseneer, 1925) or by chemical secretion (Ankel, 1937) or by both (Carriker, 1951, 1959; Ziegelmeier, 1961). Naticid gastropods make a characteristic cone-shaped or parabolic borehole (Carriker and Yochelson, 1968; Carriker, 1981). When its diameter is taken into account, the borehole is a potential source of information on, among other factors, predator size (Palmer, 1990; Kitchell et al., 1981). Stereotypy of the borehole location on prey shell over geological time in varying environments indicates a stable behavior of naticids (Sohl, 1969; Berg, 1976, 1978; Boggs et al., 1984; Kitchell, 1986, but see Arua and Hoque, 1989).

Unsuccessful attempts are preserved as incomplete and nonfunctional boreholes on the prey shell (see Anderson et al., 1991). Lack of perfection or failure in recognition can result in deviation from stereotypy and multiple boreholes (Kelley and Hansen, 2003). Deviations from stereotypy can also result from a number of other biotic factors like predator gregariousness (see Kitchell et al., 1981; Taylor et al., 1983; Anderson et al., 1991; Chattopadhyay and Baumiller, 2007 and S. Paul, pers. comm.) or non-biotic factors, like taphonomy (Chattopadhyay et al., 2006) and catastrophic physical changes leading to mass extinction (Kelley and Hansen, 1996). Mass extinction may influence drilling frequencies and predator stereotypy. For example, drilling frequencies in recovery faunas after mass extinction are greatly increased, possibly due to preferential extinction of highly escalated prey. Mass extinction also reorganizes predator-prey system and affect predator behavioral stereotypy (Kelley and Hansen, 1996).

Geographical and environmental variability also play a major role on prey-predator interaction (Kelley and Hansen, 1993). But studies are limited on the role of environmental factors on it (Allmon et al., 1990; Anderson et al., 1991; Kelley and Hansen, 1993). Significant works have been done on drilling predation through experimental studies (Paine, 1963; Moran, 1985; Yamamoto, 2004; Dietl and Herbert, 2005; Casey and

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Chattopadhyay, 2008). But behavior of predation under captivity may vary significantly; especially when its own predator is present (see Chattopadhyay and Baumiller, 2007). Presence of secondary predators also influences the feeding strategy of predatory gastropods (Kelley and Hansen, 2003). In the present study area diverse and abundant secondary predators of naticids are present. Their role in influencing in naticid-bivalve interaction has also been explored.

Kitchell et al. (1981) postulated a model based on net energy maximization gain for naticid predator that explains the preferences for prey and tested its feasibility on fossil record. Many later workers showed limitations of the model. For instance, strong surface sculptures of the prey may decrease the probability of success (Kelley, 1982). But Anderson et al. (1991) and Arua and Hoque (1989) believed that surface ornamentation may not influence the predation success. Our personal observations of naticid predation on radially costate species *Timoclea imbricata* (Sowerby, 1853) (Rao et al., 1991) also support this. There is no relation between degree of intensity of predation and surface sculpture for this species (pers. observ.). Abe (1989) found that muricid *Thais* drills prey smaller than the most profitable size, perhaps due to tidal cycles limiting which prey can be consumed during a single foraging period rather than which prey the predator is capable of manipulating. The cost-benefit could also change if the consumption time is included (Chattopadhyay and Baumiller, 2009). Kitchell et al.'s (1981) model implies that boring and consumption rates were constant. But Chattopadhyay and Baumiller (2009) showed that consumption rate vary directly with predator size. Dietl and Herbert (2005) argued that the time cost of drilling is not a simple function of prey shell thickness. They showed that edge drilling is much faster than wall drilling and it's even faster than that would be predicted if drilling time was simply a function of shell thickness. Predators probably take breaks when drilling thicker prey shells, so the relationship should not be linear (G. Herbert, pers. comm., 2010). But in the present case study we have shown that drilling takes place only on the wall and shell thickness of most frequently attacked prey size range of the two taxa are similar. We, therefore, have considered that there exists a relation between handling time and shell thickness, at least in the present study.

It appears from the above discussion that Kitchell et al. (1981) model is debatable and is constrained by many factors. This prompts us to undertake another run for testing the model in a different biogeographic area, where naticid predation on bivalve prey (one ornamented and another is non-descript) has not been studied. Given that the area is infested with naticid cannibalism and calappid crabs, it provided us opportunities to test the model in the face of steep competition and secondary predation.

The advantage of choosing intertidal samples is that they simultaneously satisfy geographical and ecological, as well as temporal (for example time averaging; Kidwell and Flessa, 1995; Roy et al., 1994; Kidwell, 2001; Yamamoto, 2004) factors of predator-prey system. The study area acts as a natural aquarium and therefore is free from any abnormal behavior of prey-predator interaction which may be shown under captivity. However, taphonomy may influence the relative abundance of drilled shells in the allochthonous assemblage. This issue has been discussed later.

Here, we have tried to see: (1) whether stability of stereotypy of borehole location is disrupted under a very stressed and complex food web, (2) predator-prey size relationship, (3) relationship between ontogenetic changes and predation intensity, (4) reliability of prey ranking with the help of predation frequency. In the present study area naticid predators are dominated by two genera, *Polinices* Montfort, 1810, and *Natica* Scopoli, 1777. Two major bivalve prey items are *Mactra luzonica* Reeve, 1854, and *Donax scortum* Linnaeus. 1758. Both prey are infaunal in shallow depth. *Mactra luzonica* is smaller (9.81 mm to 29.37 mm), while *D. scortum* is relatively larger (16.33 mm to 84.98 mm). *Mactra luzonica* is smooth-shelled, where adult *D. scortum* has co-marginal ridges with posterior spines and anterior blades. Shell thickness is larger for *D. scortum* and thickness varies with ontogeny. Since both prey live sympatrically, we assume that they are encountered simultaneously by naticid predators (see also Kitchell et al., 1981; Leighton, 2002).

It has been found that *Mactra luzonica* is more extensively predated than *D. scortum* for all size ranges. When smaller *Donax scortum* (length not exceeding the maximum length of *M. luzonica*) is studied, the predation frequency is found to be more than the subset of larger size for *Donax*. The cause has been attributed to some morphological modifications adapted by the prey during later ontogeny. It appears that the cost-benefit model is constrained by many factors including nature of ontogenetic development of the prey.

MATERIALS AND METHODS

We collected samples from intertidal areas at Chandipur, eastern coast of India (Figure 1), during January to March in 2008 and 2009. The studied area is around 5 km long, with shoreline trending NNE–SSW. The coast near the confluence of the river Burhabalang with Bay of Bengal is characterized by a wide (almost 4 km) intertidal flat with a very narrow beach (around 40 m) and bar-interbar system. The coast has mesotidal setting with semidiurnal tides (Mukherjee et al., 1987). The beach-barrier bar-estuary-tidal flat system, dominated by tide, has a prolific bio-diversity. Among mollusks around 42 genera and 56 species of gastropods and bivalves have been described (Rao et al., 1991; personal observation). We have systematically collected specimens (sample size was about 2407 for *M. luzonica* (1580) and *D. scortum* (827)). The samples are well-preserved and consisted of both articulated and disarticulated valves collected from numerous 5×5 m grids

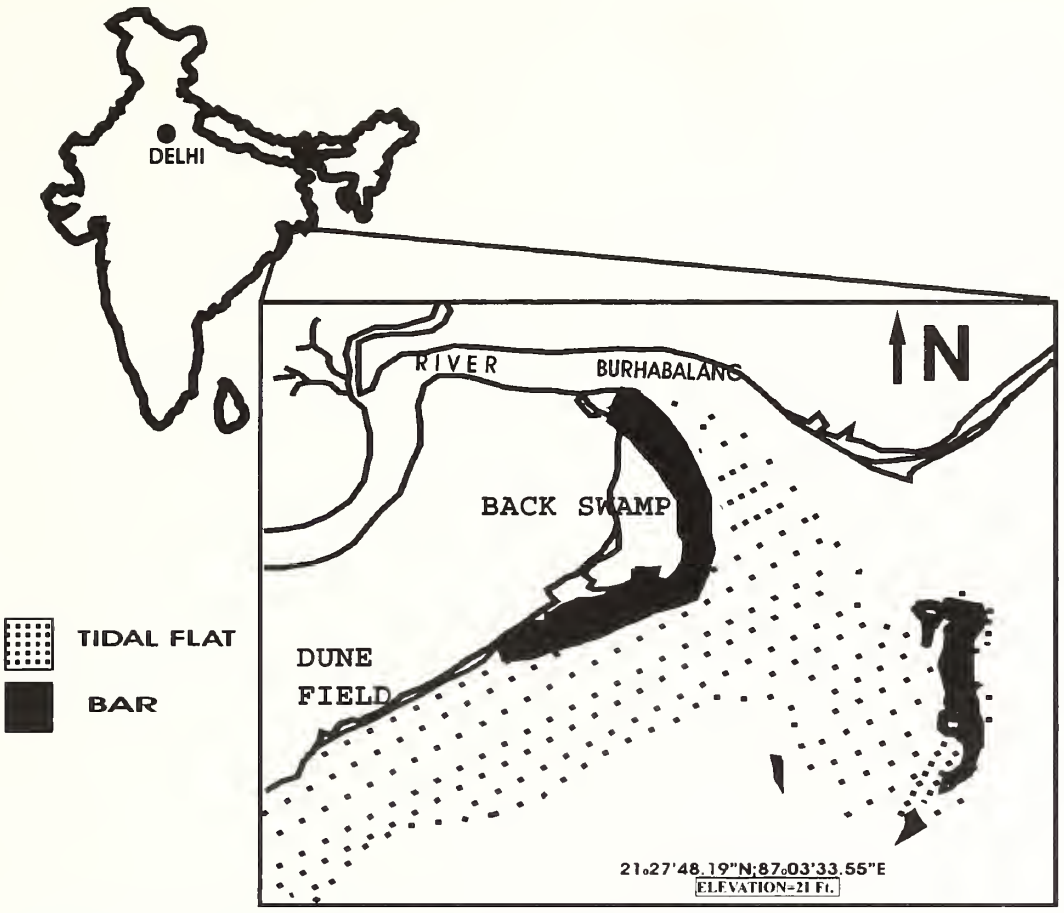


Figure 1. Chandipur beach-barrier bar-tidal flat system along the eastern coast of India.

and also randomly (for larger *D. scortum* in an unbiased way, see also Hari et al., 2009). We have only collected dead specimens. Most likely the specimens are time-averaged. Time-averaged dead assemblages are almost equivalent to fossil counterparts (Yamamoto, 2004) and could be more faithful representatives of the regional populations than living individuals (Roy et al., 1994; Kidwell and Flessa, 1995; Kidwell, 2001).

The following seven characters have been chosen for analysis and the quantifiable data thus obtained used to run cost-benefit analysis: (1) valve length of prey bivalve, (2) valve height, (3) nature of valve (left or right), (4) borehole position, (5) number of drilled samples, (6) thickness of valve at the location most frequently drilled, and (7) borehole diameter (inner and outer) made by the predators.

Other bivalve shell morphological characters including anterior and posterior length, depth of pallial sinus at different ontogenies, surface sculpture and ontogenetic changes of mode of living of *D. scortum* have also been studied to correlate them with predation frequency.

Taphonomic Bias: Taphonomy may selectively remove a particular size class from an assemblage. It shows preferences of valves in transportation especially when valves are asymmetrical (Martin-Kaye, 1951). In Chandipur, right valves of *Ostrea* spp. are rarely found. Bored valves may be differentially transported. This could either be a result of different hydrodynamic property of shells with and without boreholes (Chattopadhyay et al., 2006) or because of the fact that drilled shells are more likely to be broken during transportation (thereby lowering drilling frequency of the population) (Roy et al., 1994).

Size Selectivity: To evaluate size selectivity we have calculated Spearman rank correlation coefficient (Spearman, 1904) between prey and predator size. This has been done using the software PAST. Valve length (anterior-posterior) is used as a measure of prey size and outer borehole diameter, i.e., OBD is used as a measure of predator size (see for example, Anderson et al., 1991). Outer diameter of a series of boreholes drilled by the same predator remains relatively fixed, regardless of prey size throughout drilling phase (Kitchell et al., 1981, 1986). The data have been synthesized for the samples only having functional boreholes. For all of our statistical tests $\alpha = 0.001$.

The correlation coefficient has been calculated for (1) *Mactra luzonica*, (2) *Donax scortum* and (3) sub-set

of *D. scortum* having length not exceeding that of *M. luzonica* (see below).

Site Selectivity: Kelley and Hansen (1993) stated that if the escalation theory is true then naticid predation "may have been less stereotyped" earlier (see Arua and Hoque, 1989). Stereotypy is a predator's improved ability, which may be achieved by trial and error (Vermeij, 1983). Normally site selectivity shows a tendency of predator to choose a thin-shelled prey (Carriker, 1959; Paine, 1962) or the thinnest area of the prey shells (Kitchell, 1986). To record position of borehole, we have divided the prey valve surface into 9 sectors, for both species, following Anderson et al. (1991) (Figure 2).

Site selectivity has been tested by chi-square test using PAST. We have considered that boreholes have a random distribution throughout the valve surface (null hypothesis).

The test has been performed for: (1) *Mactra luzonica*, (2) all size ranges of *Donax scortum*, (3) *D. scortum* having length not greater than *M. luzonica* to compare the two prey when size is constant (considering predator-prey relationship holds good) and (4) all samples of both prey.

Drilling Frequency: Total number of functional boreholes is the measure of predation success. Functional boreholes are those in which IBD: OBD is >0.5 (Kitchell et al., 1986, Kelley, 1988; Anderson et al. 1991). We have used the equation (D/N)/2 to calculate drilling or predation frequency following Bambach and Kowalewski (2000) and Kowalewski (2002), where D is number of valves with complete boreholes and N is the number of valves collected.

We have measured the following: (1) valve preference for drilling, (2) size preference for both prey, (3) frequency of drilling for *M. luzonica*, (4) frequency of drilling for *D. scortum* having equivalent length of *M. luzonica*. Drilling frequency has been calculated to see whether it supported the prey ranking according to Kitchell et al. (1981) model.

Cost-Benefit Analysis: Many workers have suggested that predator-prey interaction is based on optimal foraging by the predator (Schoener, 1971, Werner and Hall, 1974; Charnov, 1976; Pyke et al., 1977; Cowie, 1977; Krebs, 1977, 1978). The most satisfactory and well-studied model for naticid predation was proposed by Kitchell et al. (1981). They suggested that predators select their prey to maximize net-energy return. Their model has been tested in fossil record (Anderson et al., 1991; Anderson, 1992). This "energy maximization model" helped us in understanding naticid behavioral pattern, as naticids rank their prey on maximum net energy return on total foraging time. These features have been incorporated in the model based on the equation:

$$E_t/T_t = E_i \cdot S_i/(H_i + R_i)$$

where E_t is total energy gained by the predator, T_t is total cost units of time to the predator, E_i is the energetic value, H_i is the handling (drilling) time cost, S_i is probability of success and R_i is the recognition time of prey "i". We have considered prey availability has no effect on prey ranking (see also Kitchell et al., 1981; Kelley and Hansen, 2006).

E_i is the approximation of energy benefit to predator resulting from prey consumption. It is estimated by the internal volume of the prey shell, i.e., equivalent to prey biomass (Kitchell et al., 1981; Powell and Stanton, 1985). Since both *M. luzonica* and *D. scortum* are equivalved, we have used single valve measurements to calculate internal volume. We have calculated internal volume of one valve by filling up with fine silver sand (conversion factor 1.626 gm/ml) and then doubled it to get the total internal volume i.e. the total biomass following Anderson et al. (1991). But 100% consumption of the prey might not occur (Edwards and Huebner, 1977; Hughes and Dunkin, 1984; Guerrero and Reyment, 1988). In our limited aquarium studies, soft parts of *Mactra* sp. including siphon, mantle etc were completely devoured by *N. tigrina*; but we did not have experimental data on *Donax scortum*. However, in the field we observed larger articulated drilled *Donax scortum* valves to possess adductor muscles and relics of mantle.

Kitchell et al (1981) considered H_i as measure of drilling time. The time cost of drilling may not always be simple function of prey shell thickness. Dietl and Herbert (2005) showed that edge drilling is faster than wall

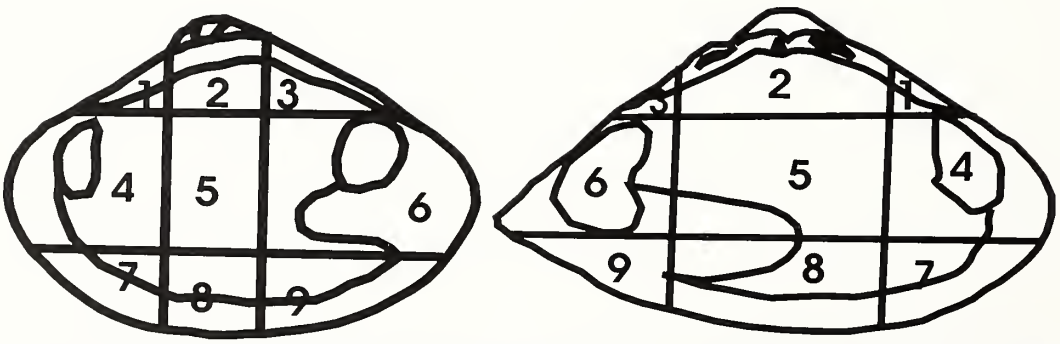


Figure 2. Nine sectors on the prey valve, drawn for analyzing site selectivity. Left *Mactra luzonica;* right *Donax scortum*.

drilling. Anderson et al. (1991) also suggested that use of thickness as a proxy for handling time may not be reliable, given that drilling rate varies across taxa. In the present case, naticids drill only on the wall and there is a strong stereotypy of drilling for both prey. The size range of the population that represents maximum predation intensity in both prey items has comparable thickness (0.18 mm for *M. luzonica* and 0.22 mm for *D. scortum*). For this we have followed Kitchell et al. (1981) and considered H_i as the proxy for drilling time in this specific case study. To measure the thickness for each prey we have taken an unbiased sample of 100 valves in which the ratio left valve:right valve is 1:1 and all size classes are represented. The number of bored samples represents the same drilling frequency of the whole population. Given that samples are easily renewable, we have broken the samples and measured the thickness at the location most frequently drilled (near umbo) using a digital calipers with measurements nearest to 0.01. We have also measured the anterior-posterior length of the valves (measure of prey size) to have an idea of change of thickness with ontogeny.

Kitchell et al. (1981) considered recognition time (R_i) of naticid predator is negligible. Anderson et al., (1991) also followed them and considered R_i as insignificant. Naticid gastropods are not visual predators. They perhaps use tactile and chemical cues (see Kitchell et al., 1981). They may not be able to differentiate between prey of same size, but of different valve thicknesses. In that case, there will be a high incidence of incomplete boreholes in thick-shelled phenotypes of the prey species. There are reports of aquarium studies where naticids grab their prey, drag it with its foot for a day, and then abandon it (G. Herbert, pers. comm.). Thus, recognition time may be substantial for drillers (see Hughes and Elner, 1979). Our direct observation on the intertidal area at low tide reveals that after initial contact, individuals of *Natica tigrina* quickly extends their feet to grab its prey, *Mactra* sp. Savazzi and Reyment (1989) reported instantaneous recognition of prey by *Natica gualteriana*, a predator also found in the present study area. Moreover, unsuccessful or incomplete boring in the studied species is extremely rare and there is no relationship between degree of shell thickness and incomplete borehole. Therefore, we have also considered the recognition time as negligible in the present case study. T_i is approximately related to H_i as the cost-benefit analysis is done within predator manipulation limit i.e. $S_i>0$.

We have measured all these parameters used in cost-benefit analysis for: (1) *Mactra luzonica*, (2) *Donax scortum*, and (3) *D. scortum* with length not greater than *M. luzonica*.

We have plotted log (thickness/ internal volume) against prey length for both prey types. According to Kitchell et al. (1981) the plotting of species-specific cost-benefit analysis provides a graphical representation of relative energetic profitability of prey species and its size classes to the predator. They noted that "Maximum E_t/T_t values represent the most vulnerable or highly ranked prey". We, therefore, have compared the result of cost-benefit analysis with the drilling frequency, which also suggests prey preference. Highest frequency of predation over a prey will have maximum E_t/T_t value over other prey.

RESULTS AND DISCUSSION

Taphonomic Control: Our samples had almost same number of left and right valves for *Mactra luzonica* (Table 1). But there was a higher incidence of occurrence of right valve in case of *Donax scortum* ($p>0.01$, Table 1). This was, perhaps, due to the fact that *D. scortum* could not be collected always through grid samples since they are relatively fewer and not evenly distributed throughout the studied area. We, therefore, have assumed (see detailed discussion in the previous section) that taphonomy has no significant role in our study (see also Boucot et al., 1958). Many articulated *D. scortum* representing different sizes (Figure 3) were also found. This clearly indicated little or no posthumous transport.

It is interesting to see that a particular size range was dominant for both prey taxa (66.5% within size range of 2.0–2.4 cm for *M. luzonica* and 56.2% for size range of 3.0–4.0 cm for *D. scortum*). But all size ranges on either side was evenly skewed (Figure 3). This spoke for normal distribution.

Site Selectivity: We have considered our observation based on the null hypothesis that prey-predator correlation exists when $p<0.0001$. In every case the correlation was significant for all size (Table 2). The area most preferred for boreholes, for both prey, was location 2. Although larger *Donax scortum* is thoroughly ornamented, location 2 is the thinnest part and carries weakest ornamentation. It is the site just below the umbo, both anterior and posterior (Table 3). Almost 95% for *Mactra luzonica* and almost 98% for *D. scortum* valves were drilled at location 2. This suggested that stereotypy is in favor of predator fitness.

Thickness Variation: When thickness of the prey at the location most frequently drilled (herein location 2, i.e., below umbo; see Figure 2) had been plotted with respect to log of body length we verified that, for *Mactra luzonica*, thickness increased with ontogeny. In later ontogeny, however, intraspecific variation of thickness

Table 1. Total number of left and right valves within total samples for both prey species.

Prey Type	Total samples	Valves	
		Left	Right
Mactra luzonica	1580	782(49.49%)	798(50.51%)
Donax scortum	827	357(43.16%)	470(56.84%)

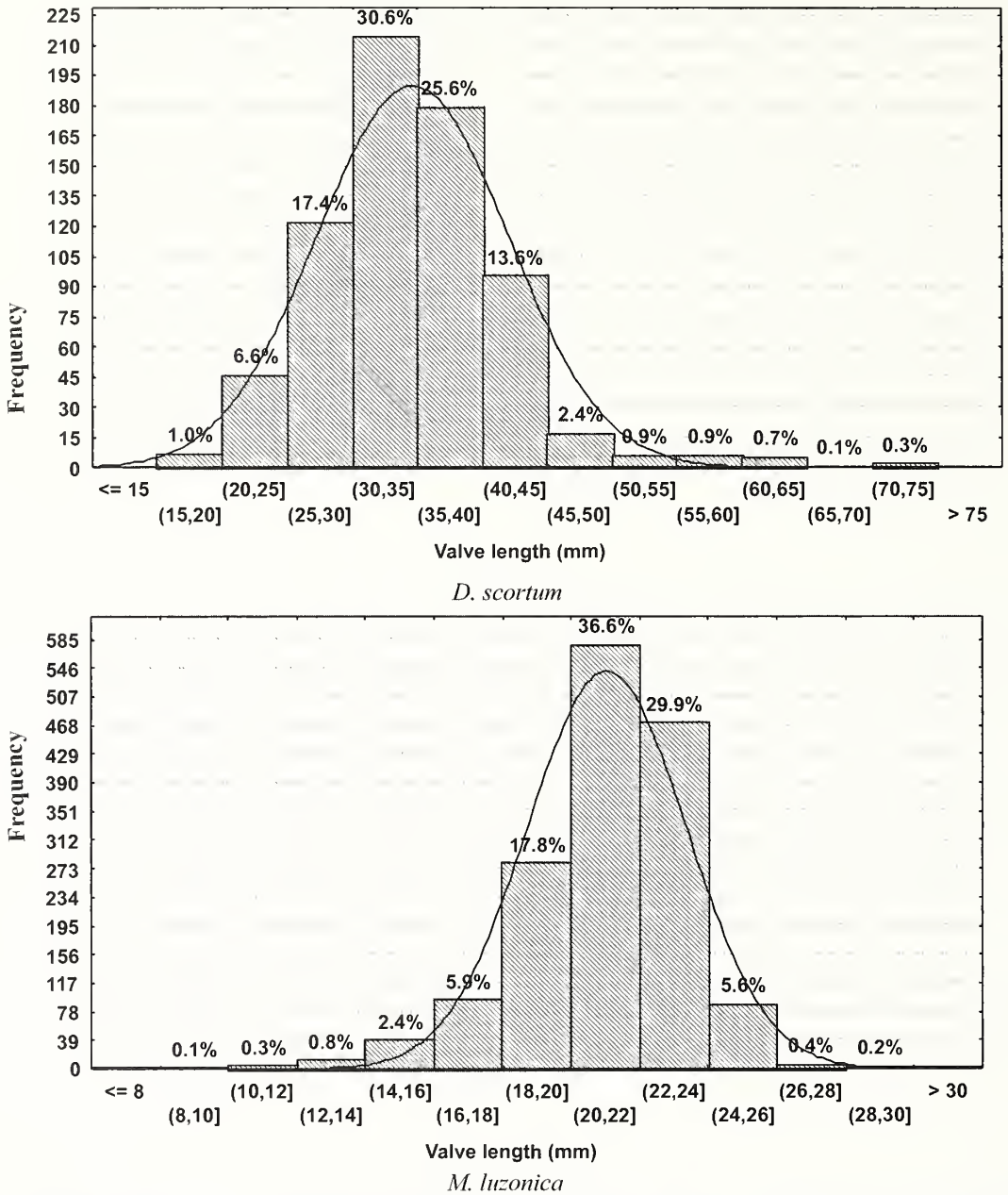


Figure 3. Available size class for two prey species at the study area. Numbers of size classes plotted against body length. Prey size show strong unimodal distribution.

Table 2. Result of borehole site selectivity test using chi-square test with eight degree of freedom.

	Excluding multiple bored valves			Including multiple bored valves		
	Sample size (bored)	X^2	p	Sample size	X^2	p
Mactra luzonica (all size class)	662	511.78	<0.0001	672	504.45	<0.0001
Donax scortum (all size class)	137	161.34	<0.0001	137	161.34	<0.0001
Donax scortum (size class not exceeding maximum size of *M. luzonica*)	42	79.355	<0.0001	42	79.355	<0.0001
All prey	799	602.12	<0.0001	809	561.93	<0.0001

Table 3. Site dependence of predators when a prey is targeted. Here location 2 is most frequently targeted for all type, all size range.

	Excluding multiple boreholes								
	Locations of boreholes								
	1	2	3	4	5	6	7	8	9
Mactra luzonica	8	630	0	1	17	3	0	1	2
Donax scortum	0	134	0	0	3	0	0	0	0

became slightly higher (Figure 4). A relatively poor correlation between shell length and shell thickness poses another problem in applying Kitchell et al. (1981) model. If the correlation is poor, then there is no way a predator can know what it is getting into when it selects a particular sized prey. A small shell could be as thick as a large shell. It is expected that selectivity for such prey should be lower when the size-thickness relationship is tight. This is also true when predator size shows poor correlation with respect to prey shell length. We have shown (see below) that as the variation of thickness during late ontogeny is not great in *M. luzonica*, the selectivity of prey has not been perturbed. But for *D. scortum* umbonal thickness remain more or less same up to 3 cm, after that thickness increase rapidly relative to length. This might have caused decrease in predation frequency for *D. scortum*.

Size Selectivity: A positive correlation indicated prey size selectivity of predators. *D. scortum* had very good correlation between OBD and prey length ($r = 0.497$, $p < 0.001$) and for *M. luzonica* it is relatively poor ($r = 0.315$, $p < 0.001$) (Table 4, see also Figure 5) since thickness shows great intraspecific variation in later ontogeny, as discussed above. Phenotypes with greater thickness may enhance resistance against wall drilling. Therefore, correlation between predator and prey size will likewise be poor, as shown in the Figure 5 (*M. luzonica*), as well as lower r value ($p < 0.001$). Since the adult size class (length: 17 mm to 25 mm) showed thickness variation less than 0.1 mm (which also represents the most abundant size class, see Figure 3), the predators mostly targeted the specimens of this size class and remain indifferent with respect to prey selection.

Drilling Frequency: Considering total mortality of studied bivalves by naticid drilling, we analyzed our samples for predation frequency. It was evident that, for *Mactra luzonica*, mortality rate was quite high (drilling frequency 24.2%, Table 5). But for *Donax scortum* mortality rate was relatively low (drilling frequency 8.79%). Against both prey, predation success was very high (i.e., predator effectiveness is almost 100%), which indicated predator perfection and adaptation in a stressed environment with a chance of semi-diurnal drying up. Moreover, predation pressure on predator was also very high, given that naticids are also victims of cannibalism and calappid crab predation at Chandipur (pers. observ.). Despite the presence of higher order predators, naticid gastropods show stereotypy in borehole location. Predation frequency here is expected to be less and there should be higher incidence of incomplete and multiple borehole (Chattopadhyay and Baumiller, 2007) and shift in position of boreholes from stereotypy (Thomas, 1976). Kitchell et al. (1981) did not mention the role of higher order predators.

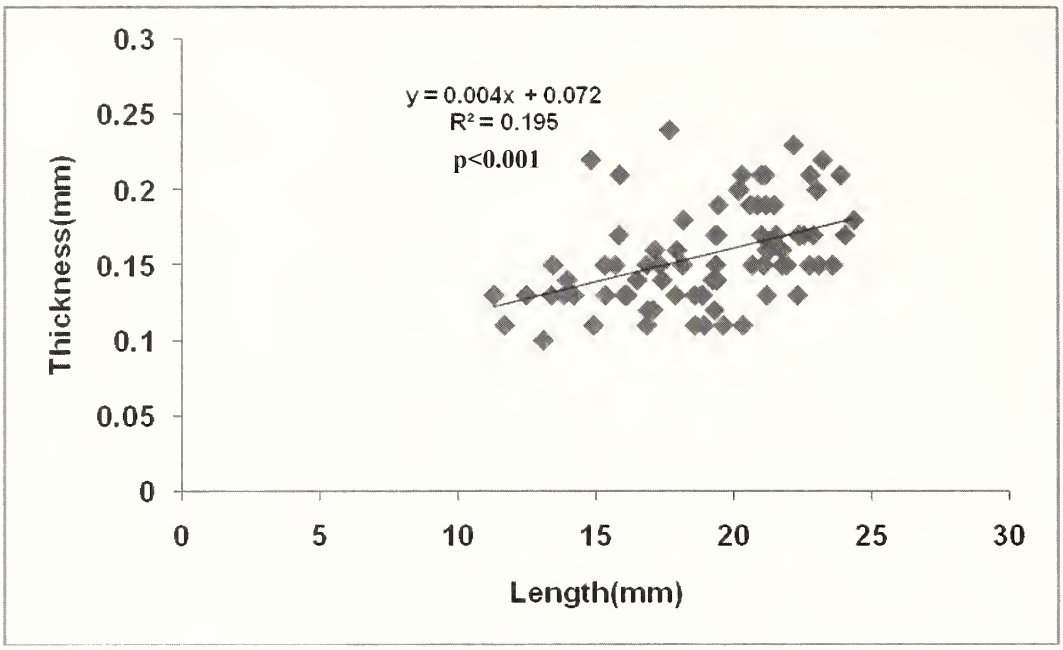
But the presence of stereotypy at Chandipur may represent a local, spatial behavioral pattern of naticids. We have encountered many naticid species performing activities such as subaerial foraging and grabbing bivalve prey on a tidal flat. During low tide, these predators are free from any danger due to secondary predators such as portunid crabs. These crabs of Bay of Bengal live in deeper water and die immediately after capture (FAO, 2010a [http://www.fao.org/fishery/species/2629/en]; FAO, 2010b [http://www.fao.org/fishery/species/2630/en]). They only reach the intertidal area at Chandipur during high tide. Savazzi and Reyment (1989) also noticed similar subaerial naticid hunting in the absence of secondary predators in the Philippines. This may be the reason of maintaining stereotypy in Chandipur prey. This may also be considered in interpreting stereotypy in fossil records.

In the present study, predators of naticid gastropods are diverse and abundant. However, we found very high frequency of predation and scarcity of incomplete borings. The reason is evident from direct observation in the vast intertidal areas at low tide, as well as from the experimental study. Naticids conceal their prey within the sediment immediately after a successful encounter. This behavior perhaps enhances the rate of predation success. We believe that attainment of perfection in drilling by achieving stereotypy involves faster drilling. Although Kitchell et al. (1981) did not consider influence of higher-ranked predators on their cost-benefit model, we here have shown that the model stands even under this complex condition.

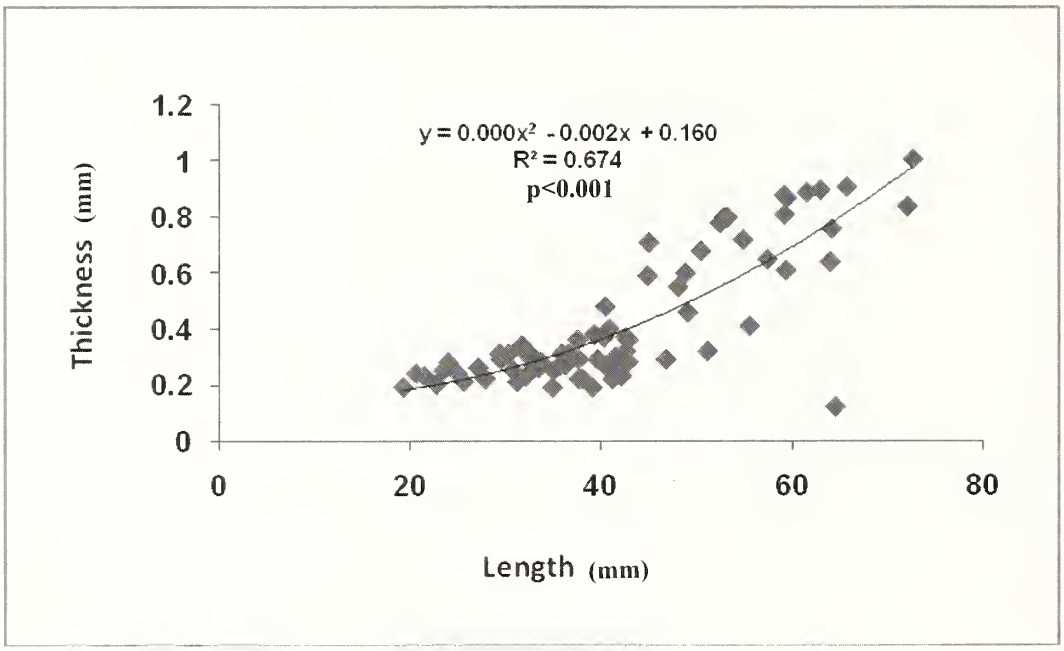
From the results (Table 5) it can be easily understood that *Mactra luzonica* was preferred over *Donax scortum*. The subset of *D. scortum* (size not exceeding that of *M. luzonica*) was studied separately. It was clear that the degree of predation was higher for this smaller size class. Number of nonfunctional and multiple boreholes (predator inefficiency) also decreased.

Neither of the prey valves was preferred for predation (Table 6). This was attributed to valve symmetry, similarity of size, shape, thickness, ornamentation, and orientation in life.

From the strongly unimodal size distribution (Figure 3) for *Mactra luzonica*, it appears that naticids would have very little to choose from total size class. When predation frequency against the available size class has been compared it is found that maximum drilling (almost 70%) is restricted within 18–24 mm size class. This class interval is also the most available class (almost 85% of all sizes). It appears that every potential food item is effective for cost-benefit within this size range.



M. luzonica

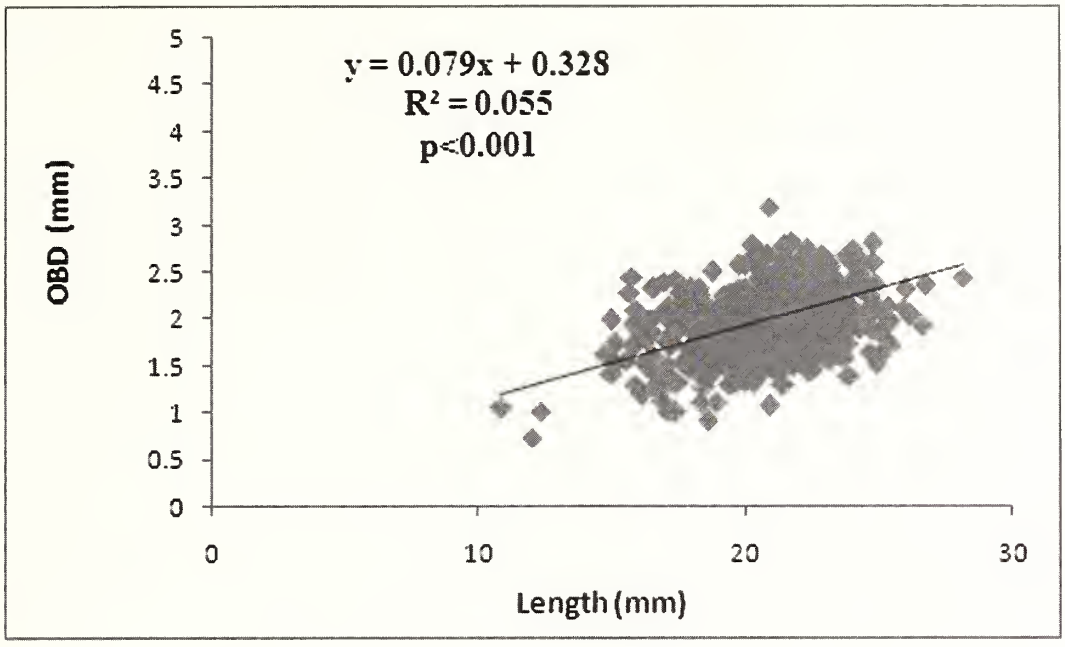


D. scortum

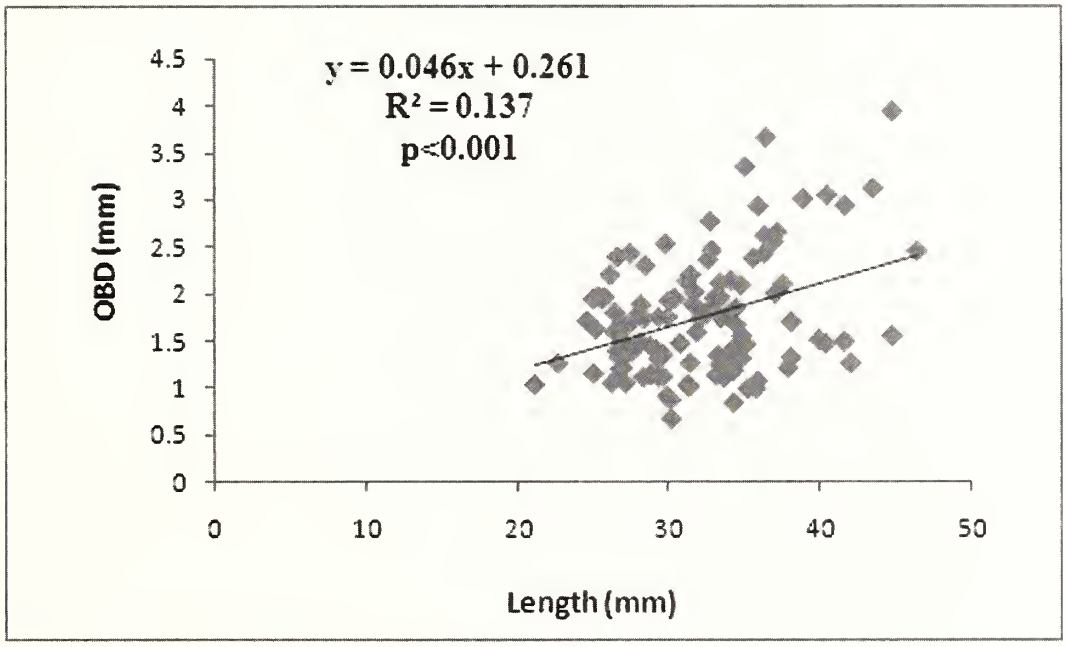
Figure 4. Change of shell thickness with ontogeny for both prey species. Length is antero-posterior shell length. For *Mactra luzonica*, the correlation between length and thickness is relatively poor.

Table 4. Values of Spearman correlation coefficient. Here, r is the correlation coefficient.

	Excluding multiple bored valves			Including multiple bored valves		
	Sample size (functional)	r	p	Sample size	r	p
Mactra luzonica	662	0.315	<0.001	672	0.309	<0.001
Donax scortum	137	0.497	<0.001	137	0.497	<0.001



M. luzonica



D. scortum

Figure 5. Predator-prey correlation where outer borehole diameter proxies for predator size and length as a proxy for prey size. OBD is outer borehole diameter.

The size range of bored valves in the two species had a size overlap between 22–28 mm (Table 6). But, the most striking aspect was that the majority of the functional boreholes in the prey were restricted in the size range that coincides with the maximum size range of *Mactra luzonica*. The number of drilled *Donax scortum* exceeding 3 cm length was rare.

Cost-benefit Analysis: Cost-benefit analysis has been done for both prey and it was interesting to see that there

Table 5. Predation frequency and valve preference for prey species, for all prey size and length not exceeding 3 cm.

Prey Type	Number of samples	Overall predation frequency	Valve preference		Unsuccessful / Nonfunctional attempt valve to valves	
			Left	Right	Left	Right
Mactra luzonica (all size class)	1580	20.95%	24.2%	25.8%	0.015%	0.005%
Donax scortum (all size class)	827	6.23%	24.76%	25.25%	0.005%	0.01%
Donax scortum (size class not exceeding 3 cm)	239	8.79%	26.19%	23.81%	0.008%	

Table 6. Valve preference of prey species for all size class.

	Total samples	functional boreholes > 0.5 R	functional boreholes > 0.5 L	functional boreholes > 0.35 R	functional boreholes > 0.35 L	Total number of bored samples	Boreholes Non functional	Boreholes multiple	Size range of predated sample (functional) (mm)
Mactra luzonica (all size class)	1580	324	315	339	322	662	14	9	10.89–28.17
Donax scortum (all size class)	827	57	75	57	75	137	10	5	21.13–46.42

existed a difference in energy values between these two species (Figure 6). Selection depends on the prey type for which energy value (E_t) is minimum, so that benefit was maximum.

According to energy maximization model of Kitchell et al. (1981), E_t/T_t will be maximum for the most favored prey. Therefore any increase in thickness at the site of stereotypy (i.e. handling time, H_i) will decrease this value (Figure 6). The trends were almost the same when we studied two prey within a size range, with maximum length 3 cm. Generally, *Donax scortum* is more costly (high thickness/internal volume) than *Mactra luzonica* (Figure 6). As a result, *D. scortum* was less frequently preyed upon. This observation corresponded well with the predation frequency data (*M. luzonica*=20.95% and *D. scortum*=6.23%).

Another factor that may be responsible for less predation on *D. scortum* is the umbonal thickness (the area most frequently drilled), which is thicker for *D. scortum* within the same size range. Average thickness was 0.35 mm for *D. scortum* and 0.16 mm for *M. luzonica*. Handling time was doubled for *D. scortum*, which would in turn increase T_i, with the result that *D. scortum* was not favored.

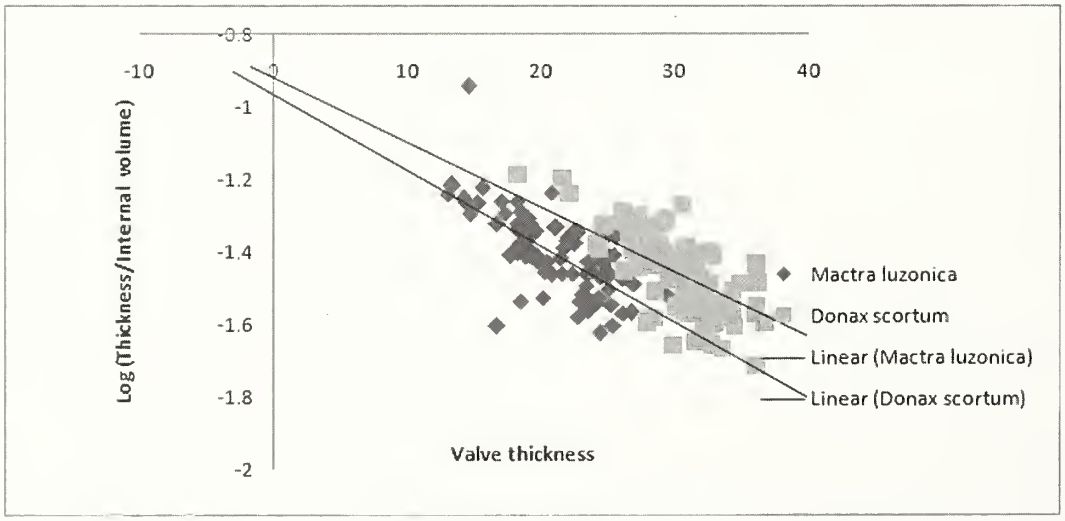


Figure 6. Comparative cost-benefit curve between two prey species within size range of 3 cm (for *M. luzonica*, $y = -0.020x-0.966$, $r^2 = 0.472$, and for *Donax scortum*, $y = -0.017x-0.922$, $r^2 = 0.302$).

Figure 7. *Donax scortum* shell showing anterior blades and posterior spines. The posterior part is swollen.

The surfaee ornamentation might be another attribute which made *D. scortum* as less favored prey. During late ontogeny, *Donax* sp. develop strong blades on the antcrior region and spines on the posterior region (Figure 7), whieh perhaps hindered predation and easy exhumation (Stanley, 1970: Savazzi, 1987). It was interesting to note that ornamentation appears only after the shell achieves 3–4 cm length. Posterior spines in many other bivalves help proteet protruding siphons; overall coarsely ornate, the shell of larger *Donax scortum* might discourage naticids to engulf it using the mesopodium.

Pereentage of eonsumption of prey biomass might be another cause (Edwards and Huebner, 1977; Guerrero and Reyment, 1988; Hughes and Dunkin, 1984). It had already been mentioned that *Mactra luzonica* was consumed totally and for *Donax scortum* this may not be so (pers. observ.). If the consumption of *D. scortum* takes longer, then it will be even costlier (for detailed diseussions on consumption rate see Chattopadhyay and Baumiller, 2009). This might have given rise to more selective predation for *M. luzonica*.

Bivariate analyses for *Donax scortum* involving anterior length against posterior length and depth of pallial sinus against valve length provided interesting results. Anterior beeame significantly larger especially at middle growth stage (3–4 cm) (Figure 8). A larger anterior region helped accommodate a large and consequently more powerful foot, which aided in efficient burrowing (Stanley, 1970). Depth of pallial sinus also inereased during ontogeny, suggesting deeper burrowing in the adult stage (Figure 8). In this condition, they are not easily available to natieid predators. These morphological ehanges might possibly have redueed predation pressure.

Mactra luzonica, on the other hand, is a shallow burrower and its burrowing depth falls within the foraging depth of naticids. Besides, smaller body size and smooth external surfaee ornamentation make it vulnerable to predation. Beeause of this *M. luzonica* is more favored prey species by the naticids in Chandipur intertidal areas.

CONCLUSION

In the present study we have tested Kitchell et al., (1981) energy maximization model on two bivalve prey of naticid predators. Our results broadly support the predietion of the model. *Mactra luzonica* (less costly prey) is found to be favored against *Donax scortum* (more costly prey).

But we feel that several other aspects should be incorporated within their model. Effect of prey availability on predation frequeney has not been considered. If an infaunal prey becomes a deeper burrower with age, it will be less available to predators and thus will increase foraging time and as well as its cost. In the present study, *Donax scortum* showed a fall in predation frequency after 3 cm length, as it burrows deeper in late ontogeny. It is shown that prey ranking is not valid after this size class, and cost-benefit analysis is supposed to be constrained by it. Therefore, in applying the model in the fossil record, we consider that eaution is to be exercised and depth of pallial sinus should be taken into account as another important variable.

Prey shell ornamentation also influence prey ranking, but this is not well tested (see Anderson et al., 1991). Although in our study we have found no significant role of shell ornamentation on predation frequeney (since stereotypy occurs in the area that bears weakest ornamentation), it still may significantly influence that. In case of a thieker prey, handling time may increase significantly if the predator takes break in the process of drilling. Consumption rate is also a function of predator size, whieh might have important implieations in cost-benefit analyses applied to varied-sized predators (Chattopadhyay and Baumiller, 2009).

Predation frequeney in presence of higher order predation may be affected (Chattopadhyay and Baumiller, 2007), but this has not been considered in this model. In our present study, stereotypy of sites along with rarity of incomplete and multiple borings on prey shell indicate that intertidal naticids are indifferent because predators arrive only with tide. We, therefore, suggest that the cost-benefit model holds even when there exists hierarchy of predators. We also conclude that secondary predation is very important to control predator effectiveness, which is evident by the presence of stereotypy of prey size and site. Drilling the thinnest part of the shell (site selectivity) quickens the handling time and results in more effective manipulation. Finally, the model of Kitchell et al (1981) has been found to be very robust

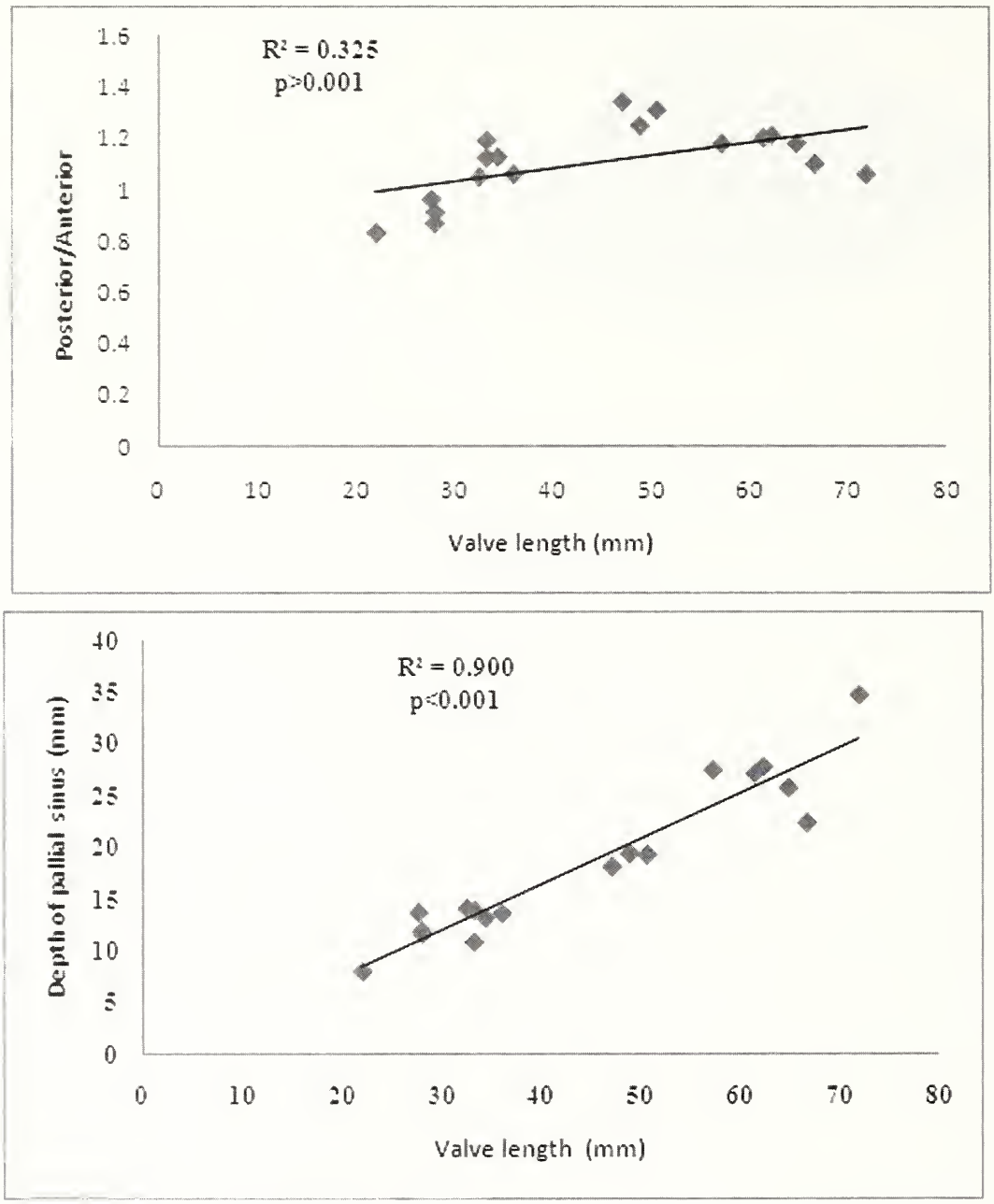


Figure 8. Relative size of anterior region increases in larger *Donax*, with a deeper pallial sinus during late ontogeny.

and well established, but when applied to fossil assemblages, the above-cited factors should be considered with equal importance.

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Research Note

Chromosomal number of two species of bivalves: *Brachidontes darwinianus* (d'Orbigny, 1842) (Mytilidae) and *Isognomon bicolor* (C.B. Adams, 1845) (Isognomonidae)

INTRODUCTION

Brachidontes darwinianus is a common species in estuaries and occurs attached to rocks in the intertidal zone of rocky shores from the state of Rio de Janeiro in Brazil, to Patagonia in Argentina (Rios, 1995), although Blanco (1966) stated that this species was found from the state of Bahia (Todos os Santos Bay), Brazil, to the mouth of the Río de La Plata, Argentina. *Brachidontes darwinianus* shows marked phenotypic plasticity, with considerable variation in shell shape, depending on where the specimens are collected. This plasticity makes shell morphology a questionable criterion for taxonomic studies (Nalesso et al., 1992; Tanaka and Magalhães, 1999).

Isognomon bicolor, a bivalve with a wide geographic distribution throughout many countries in the Americas (Domaneschi and Martins, 2002), is commonly found attached by its byssus to jetty pilings or growing in crevices on rocky shores, often in areas with strong water currents. Although most isognomonids found in Brazil have been classified as *I. alatus* and *I. radiatus*, Domaneschi and Martins (2002) stated that all of these samples effectively belong to *I. bicolor*. Indeed, the occurrence of *I. alatus* and *I. radiatus* has not been confirmed in that country.

The analysis of chromosomal numbers has been used to complement other methods of identifying species (Gosling, 1992). The aim of this work was to examine and describe the Giemsa-stained karyotype of the intertidal bivalves *B. darwinianus* and *I. bicolor*, and to compare the findings with corresponding data for other bivalve species.

MATERIALS AND METHODS

Specimens were collected from populations in Ubatuba Bay, on the coast of São Paulo state in southeastern Brazil, as follows: *Brachidontes darwinianus* from Praia Dura (23°29′36.9″ S, 45°09′54.1″ W) and *Isognomon bicolor* from Praia da Fortaleza (23°31′51.5″ S, 45°09′34.4″ W.)

These animals were maintained in the laboratory in aerated seawater at 20°C for two weeks and were fed a suspension of algal cells (*Isochrysis galbana* and *Tetraselmis suecica*) to increase the number of mitotic divisions. The voucher specimens were deposited at the Museu de Zoologia "Prof. Adão José Cardoso" (ZUEC) at the State University of Campinas (UNICAMP), São Paulo, Brazil, under the accession numbers 1444 (*Isognomon*) and 1473 (*Brachidontes*).

Chromosomal Preparation and Staining: Following treatment with colchicine (0.005%) for 10 h, the bivalves were briefly rinsed in clean seawater and the gills were removed. The tissue was immersed in 0.8% sodium citrate solution for 50 min and fixed in Carnoy's solution for 1 h at 4°C. The chromosomes were prepared by dissociating the gill tissue in 30% acetic acid on heated (43°C) slides followed by staining with 10% Giemsa solution (pH 6.8) for 10 min.

RESULTS

All *Brachidontes darwinianus* specimens had a diploid number of 2n=30 chromosomes. The karyotype consisted of two pairs of metacentric chromosomes, two pairs of subtelocentric chromosomes and 11 pairs of telocentric chromosomes (Figure 1). A diploid number of 2n=28 was observed for five individuals of *Isognomon bicolor* (Figure 2).

DISCUSSION

***Brachidontes darwinianus*:** Extensive cytogenetic studies of the Mytilidae have allowed accurate cytotaxonomic comparisons among the species in this family (Thiriot-Quiévreux, 2002). The diploid chromosome number of 2n=30 found in *Brachidontes darwinianus* has been reported in only six other mytilid species so far, namely, *Musculista senhousia* (by Ieyama, 1977), *Brachidontes recurvus* (by Diupotex-Chong, 1978), *Hormomya mutabilis* (by Ieyama et al., 1994), *Limnoperna fortunei* (by Ieyama, 1996), *Perna canaliculus* (by Libertini et al., 1996), and *Choromytilus chorus* (by Palma-Rojas et al., 1997). Only four species of the genus *Brachidontes* have been studied to date: *B. recurvus* (2n=30; mentioned above), *B. pharaonis* (2n=28; Vitturi et al., 2000), *B. minimus* (2n=28; Thiriot-Quiévreux, 2002) and *Brachidontes rodriguezi* (2n=32; Torreiro et al., 1999). The karyotype of *B. darwinianus* is unusual for bivalves because it contains only two pairs of metacentric chromosomes, with the other 13 pairs being subtelocentrics or telocentrics. The occurrence of species with subtelocentric and telocentric chromosomes is uncommon in the Mytilidae (Torreiro et al., 1999, Thiriot-Quiévreux, 2002). Overall, *Brachidontes darwinianus* showed the same chromosomal

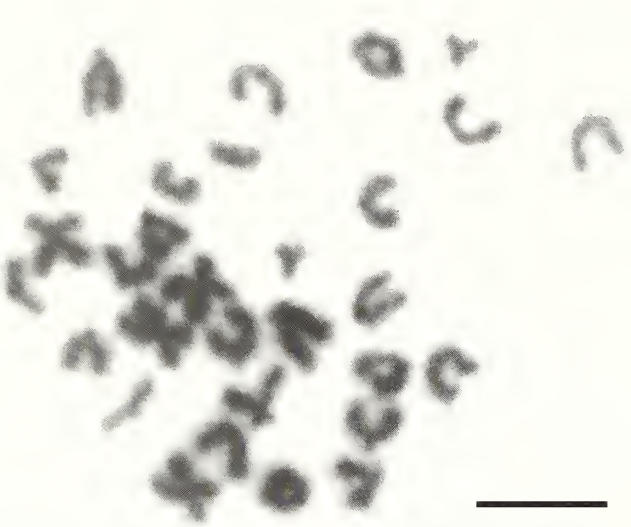

Figure 1. Mitotic metaphase of *Brachidontes darwinianus*. Scale bar = 5 μm.

number as *B. recurvus* and had a chromosomal morphology similar to that of *B. rodriguezi*, i.e. only two metacentric pairs and a predominance of subtelocentric and telocentric chromosomes.

***Isognomon bicolor*:** Squashed and air-dried preparations have been used to study chromosomes in species of the genera *Isognomon* and *Pinctada*, although the chromosomal number has been determined for only a few species of the Pterioidea (Wada, 1978; Rodríguez et al., 1983). The chromosomal number of 2n=28 here observed for this species coincided with those of the pterioidean species *I. alatus*, *Pinctada fucata*, and

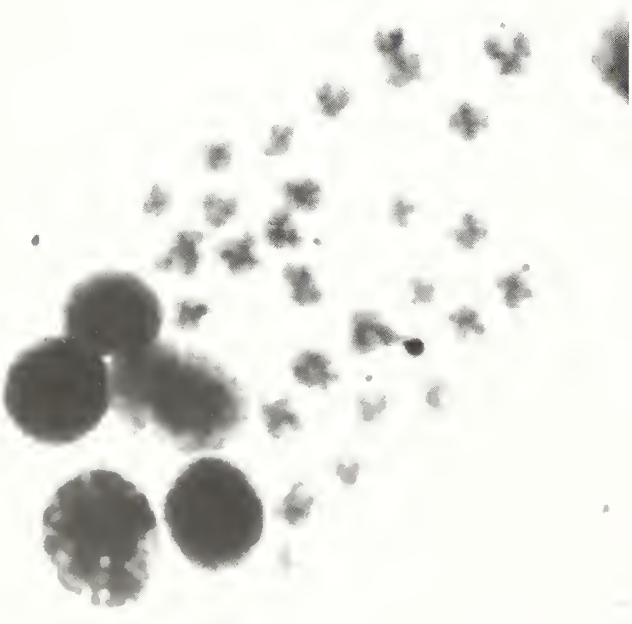

Figure 2. Mitotic metaphase of *Isognomon bicolor*, Giemsa staining. Scale bar = 5 μm.

P. imbricata. These results provide an additional example of a tendency towards a stable chromosomal number in the Isognomonidae and Pteridae, and in the superfamily Pterioidea.

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Taxonomy and distribution of fossil *Archivesica* (Bivalvia: Vesicomyidae) in Japan

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ABSTRACT

Six species of vesicomyid bivalves of the genus *Archivesica* occur in the Neogene of Japan, one further species is assigned here to this genus, but with some hesitation. Among these six species, two are herein described as new: *A. shikamai* from the Pliocene Ikego Formation on the Pacific side of Honshu and *A. kannoi* from the lower Pliocene Kurokura Formation on the Japan Sea side of Honshu; one species, the late Miocene *A. shiretokensis*, has recently been described; two species, the late Miocene to early Pliocene *A. nipponica* and the Pliocene *Archivesica* sp. were previously regarded as belonging to *Calyptogena* but are herein transferred to *Archivesica*. The extremely large Pliocene "*Calyptogena*" *bosoensis* closely resembles modern species of *Archivesica* from the western Pacific rather than species of *Calyptogena* and is herein hesitantly assigned to *Archivesica*. Compared to Paleogene species of *Archivesica* from the northern and eastern side of the North Pacific, the Neogene Japanese species differ by being larger and by lacking a lunular incision. We suggest that this group of large *Archivesica* species originated in the western Pacific during the Miocene and spread to the coast of western North America by the Pliocene. The impressive diversification of these "large *Archivesica*" species since the late Miocene might be related to the coeval decline in diversity of the elongate vesicomyid genus *Adulomya* in Japan.

Additional keywords: Neogene, new species, bivalves, *Calyptogena*

INTRODUCTION

The Vesicomyidae is a species-rich deep-water bivalve family frequently found at hydrothermal vents, cold seeps, and decaying whale carcasses. Its fossil history can be traced back to the middle Eocene (Amano and Kiel, 2007). In Japan, which has a rich record of exposed Cenozoic deep-water sediments, fossil vesicomyids are known from cold-seeps, whale-falls, and organic-rich shales. In previous studies we treated members of the genera *Adulomya* Kuroda, 1931, *Calyptogena* Dall, 1891, and *Hubertschenckia* Takeda, 1953 (Kanno et al., 1989; Amano and Kiel, 2007; Amano and Kiel, in press).

Members of the genus *Archivesica* have the largest shells among all the vesicomyids, three radiating cardinal teeth, a subumbonal pit and a shallow pallial sinus. Shells with such characteristics have been reported mainly from the Pliocene deposits in the Japan Sea side of central Honshu and the Pacific side of southwestern Honshu, and include *Akebiconcha kawamurai* Kuroda, 1943 and *Calyptogena nipponica* Oinomikado and Kanehara, 1938 and various species in open nomenclature (Majima et al., 2005). These names, however, are often used in a confusing and inconsistent manner, partly because the type material of *Calyptogena nipponica* was poorly preserved and is now lost. The purpose of the present study is to summarize the taxonomy and the distribution of the fossil Japanese species of *Archivesica* Dall, 1908 and discuss the evolutionary history of this genus.

MATERIALS AND METHODS

The new species described herein are from two Pliocene formations in Honshu, Japan (Figure 1). The specimens were collected from turbidite deposits of the Pliocene Ikego Formation at Ikego, Zushi City in Kanagawa Prefecture (Figure 1, Loc. 1). Some of these specimens had previously been described as *Calyptogena* cf. *nipponica* or *Calyptogena* sp. 1, and *C.* sp. 2 (Kanno, 1991, 1993). Further specimens were extracted from large calcareous concretion in the Pliocene part of the Kurokura Formation at Matsudai, Tokamachi City in Niigata Prefecture (Figure 1, Loc. 3). Some of these specimens had previously been described as *Calyptogena* cf. *nipponica* by Amano and Kanno (2005). All new material is housed in the Joetsu University of Education. In addition, we examined specimens identified as *A. kawamurai elongata* Ozaki, 1958 from the Pliocene Na-arai Formation at Choshi (Figure 1, Loc. 2) in Chiba Prefecture, which are housed at National Science Museum (Ozaki, 1958).

Institutional Abbreviations: ESN: Furukawa Museum of Nagoya University; IGSU: Institute of Geoscience, Shizouka University; JUE: Joetsu University of Education;

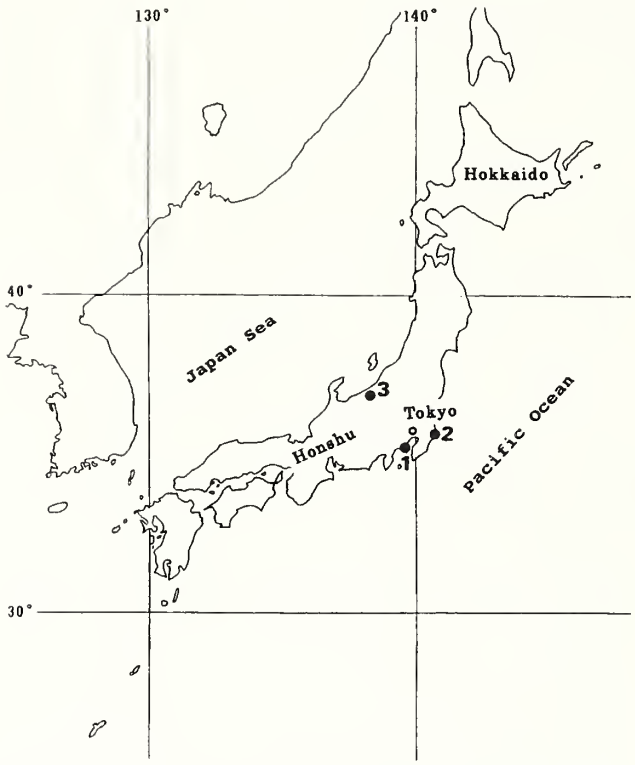


Figure 1. Locality map for fossil species of *Archivesica* in Japan.

NSMT-Mo: National Seienee Museum, Tokyo, Molluscan collection; NSM: National Seienee Museum (Paleontology); YCM-GP: Yokosuka City Museum, Yokosuka, Geology and Paleontology.

SYSTEMATICS

Family Vesieomyidae Dall and Simpson, 1901

Genus *Archivesica* Dall, 1908

Type species: *Callocardia gigas* Dall, 1896 from the Gulf of California.

Archivesica kawamurai (Kuroda, 1943)
(Figures 2–13, 19, 23)

Akebiconcha kawamurai Kuroda, 1943: 14–18, pl. 13, text-figs. 1–3; Habe, 1951: 117–118, figs. 246, 249; Ozaki, 1958: 124, pl. 3, figs.1–3, pl. 5, figs.1, 2; Habe, 1961: pl. 55, fig. 16; Shikama, 1962: 53, pl. 3, figs. 6a–b, 7a–e; Okutani, 1966: 300, pl. 28, fig. 3; Habe, 1977: 237, pl. 50, figs. 3, 4; Noda, 1980: 89–90, pl. 1, fig. 21, pl. 4, fig. 21; Tsuchida, 1986: 29–30, fig. 2; Horikoshi, 1989: 64–66, figs. 4–6; Kanno, 1993: pl. 9, figs. 1–3; Nobuhara and Tanaka, 1993: 30, 32, pl. 1, figs. 8–12; Nobuhara and Takatori, 1999: pl. 1, fig. 11.

Akebiconcha kawamurai elongata Ozaki, 1958: 123, pl. 5, figs. 3, 4, pl. 6, figs. 3–5. (*non* pl. 6, figs. 1, 2).

Akebiconcha nipponica (Oinomikado and Kanehara).—Shikama and Masujima, 1969: pl. 7, figs. 16–19.

Archivesica (*Akebiconcha*) *kawamurai* (Kuroda).—Keen, 1969: N664, figs. E138–7a–c.

Calyptogena sp. Majima et al., 1990: figs. 3A–D. (*non* figs. 3Ea,b).

Calyptogena cf. *nipponica* Oinomikado and Kanehara. Kanno, 1990: 93–95, pl. 5, figs. 1–3. (*non* pl. 6, figs. 1, 2); Kanno, 1991: pl. 2, figs. 2a–c, pl. 3, figs. 1–4.

Calyptogena solidissima Okutani, Hashimoto and Fujikura, 1992: 226–230, fig. 2–8; Okutani, 2000: 999, pl. 497, fig. 15.

Calyptogena sp. 2. Kanno, 1993: 133–135, pl. 3, fig. 1–10.

Calyptogena (*Archivesica*) *kawamurai* (Kuroda). Sasaki et al., 2005: fig. 10; Okutani, 2000: 999, pl. 497, fig. 15; Okutani, 2008: fig. 8.90.

Vesicomya (*Calyptogena*) *kawamurai* (Kuroda).—Nobuhara, 2003: fig. 3–7–12.

Type Material: Holotype NSMT-Mo 60915, off Odawara City, Sagami Bay.

Material Examined: Thirteen specimens from Loe. 1 were examined.

Remarks: The examined speeimens were treated as *Calyptogena* ef. *nipponica* or *C.* sp. 2 by Kanno (1990, 1991, 1993). They are eharacterized by having an elongate ovate shell, a shallow pallial sinus, a wide subumbonal pit and a steeply sloping and bifurcated posterior eardinal tooth in the right valve. These features elearly identify these specimens as *Archivesica kawamurai* (Kuroda, 1943). Their hinge strueture (Figures 2, 3) resembles that of the holotype of *Calyptogena solidissima* Okutani, Hashimoto and Fujikura, 1992, a speeies now considered synonym with *A. kawamurai* (Kojima et al. 2006).

As Shikama (1962) pointed out, the syntypes of *Akebiconcha kawamurai elongata* Ozaki, 1958 from the Plioeene Na-arai Formation in Chiba Prefecture are variation of this species. However, the paratype of this subspecies is from the Plioeene Ikego Formation in Kanagawa Prefecture and has a more elongate shell than the syntypes. It may belong to a new species, *Archivesica shikamai* new species, deseribed below.

Specimens reported as *Akebiconcha nipponica* from the Plioeene Imaizumi Bed in Kanagawa Prefecture (Shikama and Masujima, 1969: pl. 7, figs. 16–19) are considered here as belonging to *Archivesica kawamurai* because the illustrated specimens are indistinguishable from *A. kawamurai* by shell form and hinge strueture. Moreover, Shikama and Masujima (1969) also illustrated Reeent speeimens of *Archivesica kawamurai* as *Akebiconcha nipponica*. The original *Akebiconcha nipponica* was described from the upper Mioeene to lower Pliocene deposits in Niigata Prefecture (Oinomikado and Kanehara, 1938) and is diseussed below.

Majima et al. (1990) illustrated *Calyptogena* sp. from the Plioeene Hijikata Formation in Shizuoka Prefecture. Judging from their illustration, shell outline and hinge structure resemble that of *A. kawamurai*.

Matsushima et al. (2003) identified two specimens from the lower Pliocene Ochiai Formation in Kanagawa Prefecture as *Calyptogena* cf. *kawamurai*. Onc of the specimens (their figs. 8a, b) resembles *A. kawamurai* in its ontline and hinge structure, but the lack of information on its pallial sinus and the hinge structure of its right valve prevents us from

Figures 2–13. *Archivesica kawamurai* (Kuroda) (=*Calyptogena solidissima* Okutani, Hashimoto and Fujikura). **2, 3, 8.** All specimens are from Loc. 1. **2.** Left-valve hinge, hinge length 58.6 mm, JUE no. 15877-1. **3.** Right valve hinge, hinge length 40.1 mm, JUE no. 15877-2. **8.** Internal mold, view on right valve, length 106.0 mm, JUE no. 15877-3. **4, 5, 12.** Holotype of *Archivesica kawamurai*, length 76.4 mm, NSMT-Mo no. 60915. **4.** Left valve. **5, 12.** Right valve. **6, 7.** Hinge of holotype of *Calyptogena solidissima* Okutani, Hashimoto and Fujikura, length 128.5 mm, NSMT Mo-69675; **6.** Left valve. **7.** Right valve of which outline is shown in Figure 23. **9, 11, 13.** Syntypes of *Akebiconcha kawamurai elongata* Ozaki. All specimens are from Loc. 2. **9.** Internal mold, view on left valve, length 92.1 mm, NSM no. 4409. **11, 13.** Specimen NSM no. 4408, seen in dorsal view and view on left valve, length 85.8 mm. **10.** *Calyptogena* sp. illustrated by Majima et al. (1990, Fig. 3A). Left valve, length 63.8 mm, IGSU-M-001, Hijikata Formation.

definitely identifying it as *A. kawamurai*. The other specimen, however, (their figs. 9a, b) has many fine and regular concentric lines on its surface and a stout and posteriorly oblique middle cardinal tooth which are never seen in *A. kawamurai*.

Distribution: Pliocene: Na-arai and Kurotaki Formations in Chiba Prefecture, Ikego Formation and Imaizumi Bed in Kanagawa Prefecture, Hijikata Formation and Tamari Siltstone in Shizuoka Prefecture, Shinzato Formation in Okinawa Prefecture. Recent: Off Choshi, off Odawara, off Jogashima, Seno-Umi, Daini-Tenryu Noll, Ensei Noll, Kuroshima Noll.

Archivesica shikamai new species
(Figures 14–18, 20–22)

Akebiconcha kawamurai elongata Ozaki, 1958: pl. 6, figs. 1, 2. (*non* pl. 5, figs. 3, 4, pl. 6, figs. 3–5).
Calyptogena cf. *nipponica* Oinomikado and Kanehara.—Majima et al., 1990, fig. 3 Ea, Eb; Kanno, 1991: pl. 1, figs. 1a–c, pl. 2, fig. 1. (*non* pl. 2, figs. 2a–c, pl. 3, figs. 1–4).
Calyptogena sp. 1. Kanno, 1993: 126–132, pl. 1, figs. 1–15, pl. 2, figs. 1–12.

Diagnosis: A medium-sized *Archivesica* with elongate shell, slightly concave ventral margin, shallow pallial sinus; blunt ridge running from umbo to posterior corner; subumbonal pit wide; three radiating cardinal teeth in both valves, steeply sloping posterior tooth in right valve.

Description: Shell of medium size for genus, up to 152.4 mm long, thick-walled, elongate throughout ontogeny (height/length-ratio = 0.39–0.53), equivalve and inequilateral, weakly inflated, sculptured by growth lines only. Blunt ridge running from beak to posteroventral corner. Beak prosogyrate, situated anterior at about one-third of shell length. Anterodorsal margin broadly arched, graduating into narrowly rounded anterior margin; ventral margin slightly concave; posterodorsal margin nearly straight, gently sloping, continuing into rounded posterior margin. Escutcheon and lunule absent. Hinge plate moderately wide, with three cardinal teeth in both valves. Right valve hinge: anterior cardinal tooth (3a) thin; posterior cardinal tooth (3b) steeply oblique; central tooth (1) rather thick, vertical to hinge base; subumbonal pit wide. Left valve hinge: anterior tooth (2a) thin, oblique anteriorly, connected to stout middle tooth (2b); posterior tooth (4b) thin, oblique posteriorly; subumbonal pit wide. Nymph distinct and long, occupying two-thirds of the posterodorsal margin. Anterior adductor muscle scar subcircular; posterior one ovate; onset of pallial line near base of anterior adductor scar, obliquely crossing anteroventral shell area, pallial sinus shallow and wide; radial interior striae indistinct.

Holotype: Length 112.1 mm, height 56.1 mm, JUE no. 15878, left valve.

Paratypes: Length 106.0 mm, height 50.1 mm, JUE no. 15879-1, right valve; length 99.9 mm, height 48.3 mm, JUE no. 15879-2, right valve; length 152.4 mm, height 68.0 mm, JUE no. 15879-3, left valve; length 76.5 mm, height 35.4 mm, JUE no. 15879-4, left valve; length 110.0 mm, height 52.1 mm, JUE no. 15879-5, left valve; all from the type locality.

Type Locality: Area currently occupied by the US Army at Ikego, Zushi City, Kanagawa Prefecture.

Material Examined: Twenty-six specimens from the type locality (Loc. 1).

Remarks: When Ozaki (1958) proposed *Akebiconcha kawamurai elongata* as a new subspecies from the Pliocene Na-arai Formation, he assigned the specimens from the Pliocene Ikego Formation (Figure 16) as a paratype of the subspecies. As noted above, the syntypes of this "subspecies" can be identified as the Recent *A. kawamurai*. The paratype of *Akebiconcha kawamurai elongata* has a more elongate shell than the syntypes of *A. kawamurai elongata* and the Recent specimens of *A. kawamurai*. Moreover, this specimen was collected from the same Ikego Formation as the present new species. Thus, the paratype can be included into the present new species.

Comparison: *Archivesica shikamai* closely resembles *A. kawamurai* in the arrangement of cardinal teeth in the right valve, but differs from it by having a more elongate shell (see Figure 24) and a wider subumbonal pit. The type material of *A. shikamai* was previously described and illustrated by Kanno (1991, 1993) as *Calyptogena* cf. *nipponica* and *Calyptogena* sp. 1. from the type locality where it co-occurs with *Archivesica kawamurai*. Such a co-occurrence of two large *Archivesica* species at a single locality resembles the co-occurrence of *A. soyoae* (Okutani) and *A. okutanii* (Kojima and Ohta) in Sagami Bay today.

Distribution: Pliocene Ikego Formation in Kanagawa Prefecture.

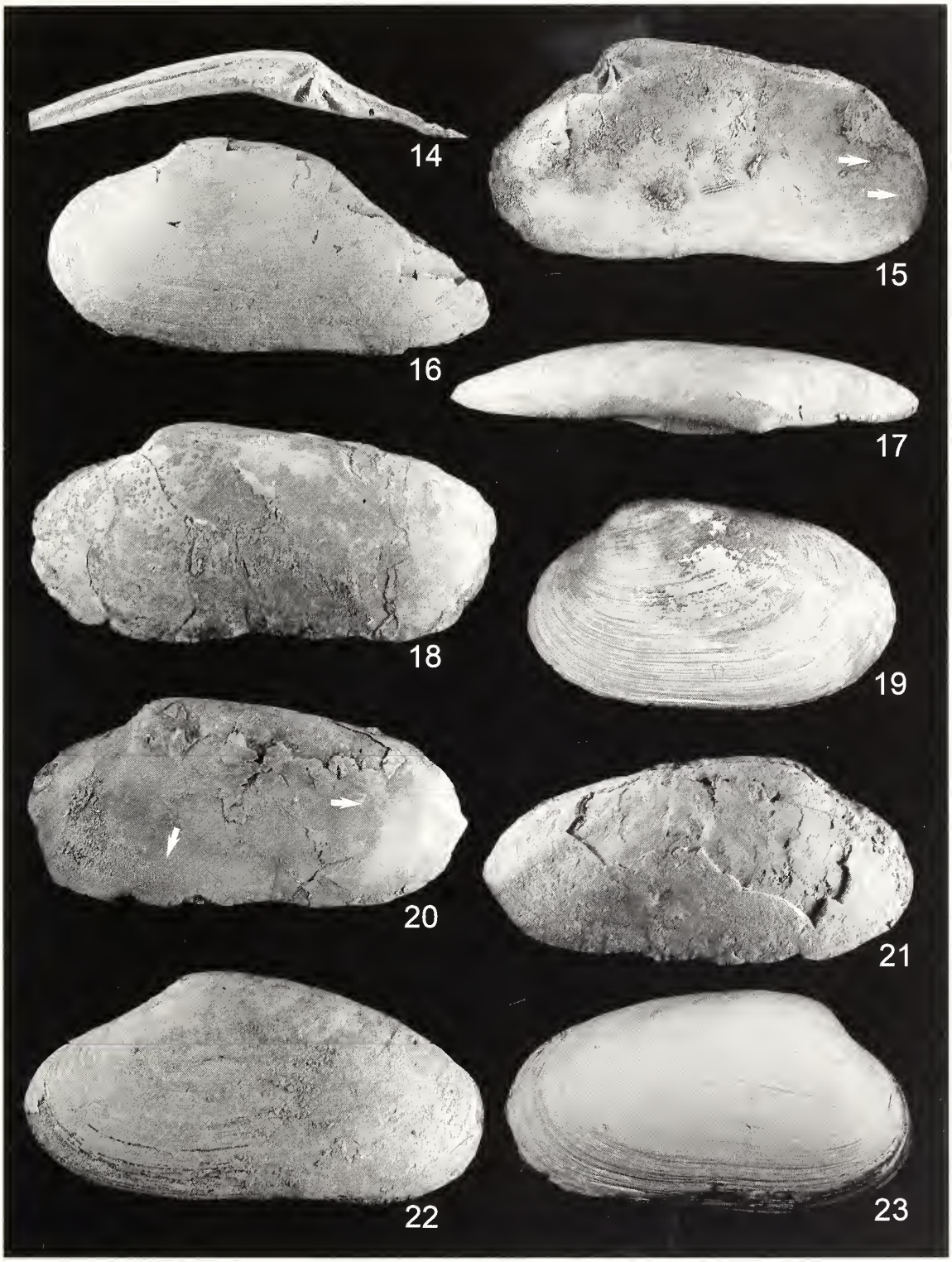
Etymology: Named after the late Emeritus Prof. Tokio Shikama (Yokohama National University), a molluscan paleontologist, who also studied the molluscan fauna from the Ikego Formation.

Archivesica kannoi new species
(Figures 25–31)

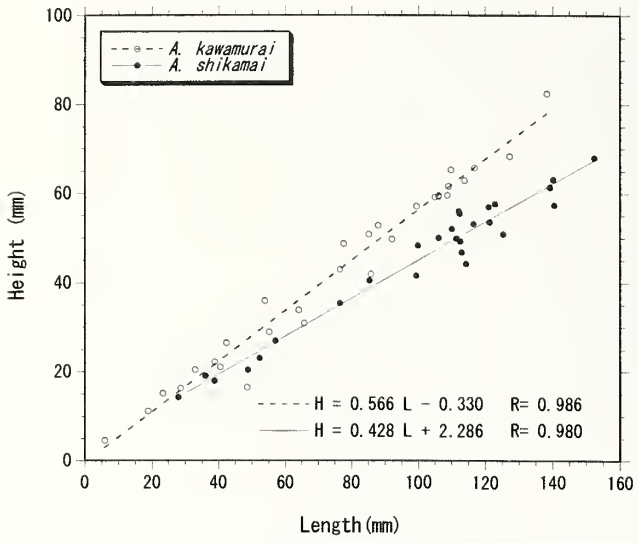
Calyptogena nipponica Oinomikado and Kanehara.—Kanno, 1993: pl. 7, figs. 4–9; Amano, 1994, pl. 2, figs. 1, 3, 8, 11.
Calyptogena cf. *nipponica* Oinomikado and Kanehara.—Amano and Kanno, 2005: 207–208, figs. 4, 5, 11–13.

Diagnosis: A medium-sized *Archivesica* with elongate quadrate shell, very shallow pallial sinus; subumbonal pit small but deep; three radiating cardinal teeth in both valves.

Description: Shell of moderate size for genus, up to 124.6 mm long, thin-walled, elongate quadrate in adults (height/length-ratio = 0.48–0.57; length>40 mm; Figure 32), elongate ovate in juvenile (height/length-ratio = 0.49–0.76; length<40 mm), equivalve and inequilateral, moderately inflated, sculptured only by fine growth lines.



Figures 14–23. *Archivesica shikamai* new species. All specimens are from Loc. 1. **14, 17, 22.** Holotype, length 112.1 mm, JUE no. 15857. **14.** Right-valve hinge, hinge length 59.4 mm. **17.** Dorsal view. **22.** Left valve. **15.** Paratype, length 106.0 mm, JUE no. 15879-1, inner part of left valve, white arrows indicating the pallial sinus. **18.** Paratype, internal mold, length 76.5 mm, JUE no. 15879-4, left valve. **20.** Paratype, internal mold, length 110.0 mm, JUE no. 15879-5, left valve, white arrows indicating pallial line and sinus. **21.** Paratype, length 99.9, JUE no. 15879-2, right valve. **16.** Paratype of *Akebiconcha kawamurai clongata*, length 112.3 mm, NSH 4441. **19, 23.** *Archivesica kawamurai* (Kuroda). **19.** Holotype of *Archivesica kawamurai*, length 76.4 mm, NSMT-Mo no. 60915, left valve. **23.** Holotype of *Calyptogena solidissima* Okutani, Hashimoto and Fujikura, length 128.5 mm, NSMT Mo-69675, right valve.



Figures 24. Diagram showing height/length-ratios of *Archivesica kawamurai* and *A. shikamai* new species

Beak prosogyrate, situated anteriorly at about one-fourth of shell length. Antero-dorsal margin broadly arcuated, graduating into narrowly rounded anterior margin; ventral margin broadly arcuated; posterodorsal margin straight, gently sloping, graduating into rounded posterior margin. Escutcheon and lunule absent. Hinge plate with three cardinal teeth in both valves. Right valve hinge: anterior cardinal tooth (3a) very thin along dorsal margin; posterior cardinal tooth (3b) oblique; central tooth (1) rather thick, vertical to hinge base; subumbonal pit narrow. Left valve hinge: anterior tooth (2a) thin, oblique anteriorly, connected to stout middle tooth (2b); posterior tooth (4b) thin, oblique posteriorly; subumbonal pit narrow and shallow behind posterior tooth. Nymph distinct, occupying two-thirds of the posterodorsal margin. Anterior adductor muscle scar pear-shaped; posterior one ovate; deep groove observed just behind anterior adductor scar and just before posterior scar. Pallial line starts near posteroventral corner of anterior adductor scar, running mostly parallel to ventral shell margin, pallial sinus varying from very shallow to shallow. Inner shell surface finely and weekly crenulated.

Holotype: Length 124.6 mm, height 66.3 mm, JUE no. 15880, left valve.

Paratype: Length 62.6 mm+, height 37.9 mm, JUE no. 15881-1, right valve; length 48.7 mm, height 28.1 mm, JUE no. 15881-2, right valve; length 79.1 mm+, height 45.9 mm, JUE no. 15881-3, left valve; length 38.4 mm, height 18.9 mm, JUE no. 15881-4, right valve; length 37.4 mm, height 20.9 mm, JUE no. 15881-5, right valve.

Type Locality: 1 km west to Matsudai, Tokamachi City, Niigata Prefecture (Loc. E2 by Amano and Kanno, 2005).

Material Examined: Thirty-eight specimens from the type locality (Loc. 3).

Remarks: *Archivesica kannoi* new species was described or illustrated as *Calyptogena nipponica* or *C.* cf. *nipponica* by Kanno (1993), Amano (1994) and Amano and Kanno (2004). However, the hinge of the type *C. nipponica* can partly be observed and the condition of pallial line is unknown. Moreover, the type material of *Calyptogena nipponica* was probably destroyed during World War II. Thus, it is difficult to compare this new species to *C. nipponica*.

Comparisons: *Archivesica kannoi* new species is most similar to *A. shiretokensis* (Uozumi, 1967) from the upper Miocene Rusha Formation in Hokkaido regarding size and hinge structure. *Archivesica kannoi* differs from *A. shiretokensis* by having a less concave ventral margin, a vertical middle tooth in the right valve and a very shallow pallial sinus. The Recent species, *A. soyoae* (Okutani, 1957) can be distinguished from *A. kannoi* by its slightly concave ventral margin, its slightly bifid posterior tooth in the right valve, and its deeper pallial sinus. Some specimens have a "broad" or secondary pallial line running closer to the shell margin and roughly parallel to the real pallial line except for the posterior area where it does not form a pallial sinus but ends at the posterior side of the posterior adductor scar (see Figure 31). This "broad" or secondary pallial line can also be seen in other large *Archivesica* species such as *A. kawamurai* (see Figure 12 of the holotype of the latter species).

Distribution: Lower Pliocene part of the Kurokura Formation in Niigata Prefecture.

Etymology: Named after the late Emeritus Prof. Saburo Kanno (University of Tsukuba and Joetsu University of Education), a molluscan paleontologist, who studied the vesicomyids from the Kurokura Formation.

Archivesica nipponica (Oinomikado and Kanehara, 1938)

Calyptogena nipponica Oinomikado and Kanehara, 1938: p. 677–678, pl. 21, figs. 1–5.
non Akebiconcha nipponica (Oinomikado and Kanehara); Shikama and Masujima, 1969: pl. 7, figs. 16–19.

Type Material: The type material was deposited in the Imperial Geological Survey of Japan, and was destroyed according to Hatai and Nisiyama (1952).

Remarks: Oinomikado and Kanehara (1938) described *Calyptogena nipponica* from the lower Pliocene "Ushigakubi bed" [= upper part of Araya Formation; Kobayashi et al., 1991] and from the cuttings of a well dug into the upper Miocene? "Kubiki Series". Regarding its size (holotype length 115.4 mm), outline, the three strong, radiating cardinal teeth, and the narrow and shallow subumbonal pit in the right valve, this species is similar to *Archivesica soyoae* and presumably belongs to the genus *Archivesica*. The posterior cardinal tooth of the right valve of *Archivesica nipponica* does not bend towards the anterior, which precludes its placement within *Calyptogena*. However, most inner features

Figures 25–31. *Archivesica kannoi* new species. All specimens are from Loc. 3. **25.** Paratype, hinge length of left valve 33.8 mm, JUE no. 15881-3. **26, 27.** Paratype, JUE no. 15881-1. **26.** Right valve hinge, hinge length 24.0 mm. **27.** Right valve, length 62.6 mm+. **28.** Paratype, internal mold, length 38.4 mm, JUE no. 15881-4, left valve, white arrow indicating the very shallow pallial sinus. **29.** Paratype, internal mold, length 48.7 mm, JUE no. 15881-2, right valve, white arrow indicating the very shallow pallial sinus. **30.** Holotype, internal mold, length 124.6 mm, JUE no. 15880, right valve. **31.** Paratype, internal mold, length 37.4 mm, JUE no. 15881-5, left valve, white arrow indicating the shallow pallial sinus.

except for the ill-preserved right valve hinge are unknown. The type locality has been visited twice by the senior author but new material of *Archivesica nipponica* was not found. Thus its characters and relationships to other vesicomyids remain unclear.

Distribution: Upper Miocene? "Kubiki Series" in Niigata Prefecture; Lower Pliocene part of the Araya Formation in Niigata Prefecture.

Archivesica shiretokensis (Uozumi, 1967)

"*Calyptogena*" *shiretokensis* Uozumi in Uozumi and Ishikawa, 1967: p. 44, fig. 3

Archivesica shiretokensis (Uozumi).—Amano and Suzuki, 2010: 165–171, fig. 2 A–J.

Holotype: Type specimens were assigned and illustrated by Uozumi (1967) but their repository is unknown.

Remarks: Recently Amano and Suzuki (2010) collected topotype specimens and redescribed *Archivesica nipponica* in detail.

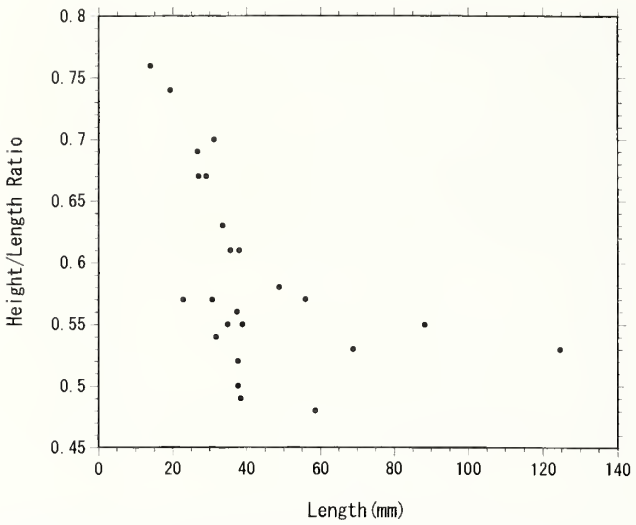


Figure 32. Relationship between shell length and the height/length ratio of *Archivesica kannoi* new species.

Distribution: Upper Miocene Rusha Formation in Hokkaido.

Archivesica sp.

Calyptogena sp. Nobuhara and Takatori, 1999: 145, Pl. 1, figs. 5–10.

Specimens: ESN nos. 2695–2700.

Remarks: This species has a large shell exceeding 130 mm in length, a posteriorly oblique posterior tooth (3b) in the right valve on which a distinct groove can be recognized, and a deep subumbonal pit. As Nobuhara and Takatori (1999) pointed out, these features are recognized in *A. soyoae* and *A. okutanii* (Kojima and Ohta, 1997). However, due to the poor preservation of the sixteen specimens collected and illustrated by Nobuhara and Takatori (1999), a species-level identification is currently not possible.

Distribution: Pliocene Horinouchi Formation in Shizuoka Prefecture.

?Archivesica bosoensis (Kanie and Kuramochi, 2001)

Calyptogena sp. Majima et al., 1992: p. 373–376, figs. 3.1–3.3.
Calyptogena (*Ectenagena*) sp. Kanie et al., 1997: p. 794–795, figs. 2.1a–c.
Calyptogena bosoensis Kanie and Kuramochi, 2001: p. 6–8, figs. 3.1–3.2, 4Cb.

Holotype: YCM-GP no. 1143.

Paratype: YCM-GP no. 1144.

Remarks: *?Archivesica bosoensis* reaches 235 mm in length, which is close to the maximum size of *Archivesica*. Kanie and Kuramochi (2001) pointed out that *?A. bosoensis* is very similar in shape to the Recent *A. similaris* Okutani, Kojima, and Ashi, 1997, except for its much larger size. Another species that is similar in shape and size is the Recent "*Calyptogena*" *garuda* from 2064 to 2137 m depth off Java, Indonesia (Okutani and Soh, 2005). Judging from its size and outline, *?Archivesica bosoensis* probably belongs to the genus *Archivesica*, but this assessment has to remain tentative until better preserved material becomes available.

Distribution: Pliocene Shiramazu Formation in Chiba Prefecture.

DISCUSSION

The genus *Archivesica* first appeared in Japan in the late Miocene with two species; an additional four species appear in the Pliocene (Table 1, Figure 33). Today, eight species and one subspecies of *Archivesica* are living around the Japanese Islands (Sasaki et al., 2005; Okutani et al., 2009). On the northern and eastern side of the Pacific *Archivesica* has a much longer fossil record, ranging back to the middle Eocene of Washington State and the Oligocene of Alaska (Amano and Kiel, 2007; Kiel and Amano, 2010). But these Palcogene species are much smaller (max. 48 mm) than those reported here from the Japanese Neogene (112 to 235 mm) and most have a lunular incision, a feature not seen in the large Neogene species of *Archivesica*. The large vesicomyids known

Table 1. Age and characteristics of fossil *Archivesica* species in Japan. Position of umbo is expressed as percentage along shell length from anterior end.

Species	Age	Maximum length (mm)	Shell shape	H/L	Position of umbo (%)	Steeply oblique 3b tooth	Bifid 3b tooth	Subumbonal pit	Pallial sinus
A. shiretokensis	Late Miocene	152.6	elongate-elliptical	0.44–0.48	16–22	–	+ (weak)	narrow, shallow	shallow
A. nipponica	Late Miocene–Early Pliocene	115.4	elongate-elliptical	0.40	25–33	–	–	narrow, shallow	?
A. kannoi n. sp.	Early Pliocene	124.6	elongate-quadrate	0.48–0.76	17–33	–	–	narrow, shallow	very shallow
A. shikamai n. sp.	Pliocene	152.4	very elongate-elliptical	0.39–0.53	27–40	+	–	wide	shallow
A. kawamurai	Pliocene–Recent	138.9	elongate-elliptical	0.54–0.62	26–36	+	+	wide	shallow
A. sp.	Pliocene	>130.0	whole outline unknown	?	?	–	+	narrow, deep	?
A.? bosoensis	Pliocene	235.0	very elongate-elliptical	0.35–0.38	23–26	?	?	?	?

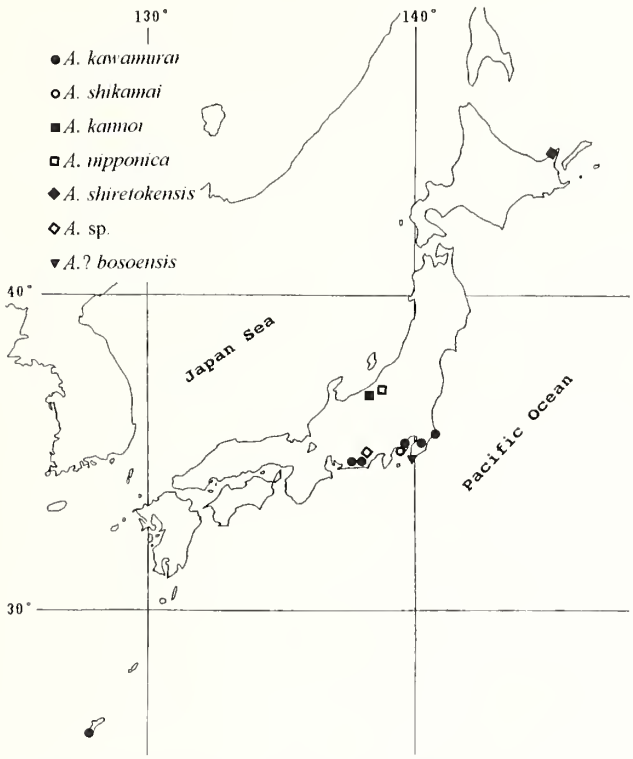


Figure 33. Distribution of fossil *Archivesica* in Japan. *A. shiretokensis*: late Miocene; *A. nipponica*: late Miocene to early Pliocene; *A. kannoi*: early Pliocene; *A. shikamai*: Pliocene; *A.* sp.: Pliocene; *?A. bosoensis*: Pliocene; *A. kawamurai*: Pliocene to Recent.

from Cenozoic seep deposits in the Caribbean region (Gill et al., 2005; Kiel, 2007; Kiel and Peckmann, 2007) are of the elongate type around the genus *Adulomya*. The earliest record of a "large *Archivesica*" from the American Pacific coast is *A. gibbera* from the early Pliocene of California (Crickmay, 1929; Squires, 1991). This pattern of occurrence suggests that the "large *Archivesica*" originated in the western Pacific sometime during the middle/late Miocene and subsequently spread eastward to North America. However, because no vesicomyids have been reported so far from the late Miocene of western North America, this scenario remains tentative. Interesting in the context of the dispersal history of the "large *Archivesica*" in the Pacific are the "large vesicomyids" recently reported from lower Pliocene cold seep deposits in the eastern central Philippines (Majima et al. 2007), because of the similarities between the Pliocene Japanese *?Archivesica bosoensis* and the modern Indonesian *A. garuda*.

The diversification history of the Neogene "large *Archivesica*" in Japan is in an interesting contrast to the evolutionary history of the large, elongate vesicomyid genus *Adulomya*. *Adulomya* first appeared in Japan in the early Miocene, it was present with five species during the early and middle Miocene, and experienced a steep decline in diversity through the late Miocene and Pliocene (Amano and Kiel, in press). This decline in diversity might relate to the rise of the "large *Archivesica*" from the late Miocene onward. Different again is the history of *Calyptogena* in Japan, which first appeared with one species in the late Miocene (Kanno et al., 1989) and maintained a low diversity until today (Sasaki et al., 2005; Okutani et al., 2009).

Both fossil and Recent records of *Archivesica kawamurai* are confined to the accretionary prism on the Pacific side of southwestern Honshu, an area with many cold-seep sites (Fujioka and Taira, 1989; Kojima, 2002), indicating that *A. kawamurai* has not changed its area of distribution since the Pliocene. Such distribution pattern might relate to stable environmental conditions in this area: the basic tectonic framework of Japan has not changed from the late Miocene to the Recent (e.g. Iijima and Tada, 1990) probably resulting in constant methane seepage along the accretionary prism off southwestern Honshu.

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Descriptions and illustrations of some new and poorly known turrids of the tropical northwestern Atlantic. Part 1. Genera *Buchema* Corea, 1934 and *Miraclathurella* Woodring, 1928 (Gastropoda: Turridae: Crassispirinae)

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ABSTRACT

Descriptions and illustrations are presented for four small, less than 12 mm in length, crassispirine turrids from the southeastern Caribbean, three in the genus *Buchema* Corea, 1934 and one in *Miraclathurella* Woodring, 1928. One of the three *Buchema* is described for the first time. The other two, *Buchema bellula* (E.A. Smith, 1882) and *Buchema primula* (Melvill, 1923), are redescribed because they are relatively unknown, and lack published photographs and adequate description. Their identification is compounded by the existence of a hitherto undescribed small *Buchema* that is similar in appearance, *Buchema nigra* new species, and by similar looking small *Crassispira* in the subgenus *Monilispira* Bartsch and Rehder, 1939 that will be addressed in a later paper. The fourth small crassispirine, *Miraclathurella peggywilliamsae* new species, is only the second known member presently placed in this genus in the tropical northwestern Atlantic. Variation in form of the four species is described.

Additional keywords: Taxonomy, systematics, new species, gastropods, Neogastropoda, western Atlantic

INTRODUCTION

This is the first in a series of papers covering small crassispirine turrids. Turrids are among the least understood of the tropical northwestern Atlantic (TNWA) mollusks for a number of reasons. They are very speciose, small, scarce, and for some, incompletely described by their original authors. Relative inaccessibility of types, such as those deposited in the British Museum of Natural History, has contributed to their anonymity. The focus of this part of the series is primarily on the genus *Buchema* Corea, 1934, most of whose members are poorly known. Scarce reports of *Buchema* in the literature offer little additional new descriptive or biogeographic information beyond what is given in the original descriptions. Reports in which *Buchema* have appeared include surveys (Altena, 1975; Olsson and McGinty, 1958; Ekdale, 1974; Absalão et al., 2005), and identification guides (Warmke and Abbott, 1961; Abbott, 1974; Rios, 1975, 1985, 1994, 2009; Humfrey, 1975; Kaicher, 1984; Díaz and Puyana, 1994; Williams, 2005, 2006, 2009). Maes (1983) published new information about *Buchema interstrigata* (E.A. Smith, 1882), for a population in a shallow water community at White Island, British Virgin Islands, and described differences between this species and *Buchema interpleura* (Dall and Simpson, 1901). These two larger, better known species are not treated in this work. Instead two smaller, little known ones, *Buchema bellula* (E.A. Smith, 1882) and *Buchema primula* (Melvill, 1923), are re-described. *Buchema bellula* was collected as early as 1964 (based on data labels of specimens at the Academy of Natural Science of Philadelphia). More recently, it has been found by diver-collectors multiple times, and sufficient material has become available to improve its description, describe its variability, and better illustrate the species. *Buchema primula* is very close in appearance to *B. bellula* and similar to another small species described here for the first time, *Buchema nigra* new species. These two species, *B. primula* and *B. nigra*, have also been found in multiple locations by different explorers. Another two, very similar but as yet undescribed *Buchema*, will be mentioned and illustrated, although not fully described because of insufficient specimens. The species treated here share important characteristics of the genus *Buchema*, in addition to the characteristics of the subfamily. Discussing them together here will better illustrate these shared characteristics but also their individual uniqueness.

The last species described in this paper, a Recent species, is a member of the genus-group *Miraclathurella* Woodring, 1928, which was erected for fossil species from the Bowden Formation of Jamaica. It is similar in some basic sculptural elements and overall appearance to small *Buchema*, so is included here for comparison purposes. It has also been taken from several different localities to allow a fair picture of its variability and distribution.

Species are treated systematically, including known synonyms, description, range, distinguishing characteristics, and variability.

MATERIALS AND METHODS

The literature of TNWA crassispirines was reviewed for descriptions, synonymy, and reported occurrences. A list of reported localities was developed for previously described species using published sources and data slips of museum lots.

Specimens for study were acquired from personal sampling trips, private collections, and from commercial dealers. In all cases, only the shell is used for identification and descriptive purposes. To supplement personally acquired material, museums lots were examined to gain a better understanding of a species variability and to identify characters that are consistent within and best distinguish it from other species. Collections in the National Museum of Natural History (USNM), Washington DC, and the Academy of Natural Science of Philadelphia (ANSP) were examined. Specimens of previously described species were compared to type material located at the British Museum of Natural History (BMNH).

Measurements of overall shell dimensions were taken to the nearest 0.1 mm employing an ocular micrometer mounted in a Bausch & Lomb stereo binocular dissecting microscope. Photographs of all species were taken employing a stand-mounted Nikon® D-90 digital camera with an AF-S VR Micro-Nikkor 105 mm f/2.8G macro lens fitted with one or more extension tubes (12, 20, or 36 mm) to obtain the largest image. Light was provided by the Nikon close-up remote kit with dual remote speedlights attached to a front-mounted ring. Individual specimen photos were cropped and sized appropriately for the plates using Adobe® Photoshop® CS2 computer software.

Types and voucher specimens originally in the possession of the author have been deposited in the ANSP, The Bailey Matthews Shell Museum (BMSM), Florida Museum of Natural History (FLMNH), and USNM. Catalog numbers are given in the text. A few paratypes remain in private collections for deposition elsewhere at a later time. Saint Vincent and the Grenadines is herein abbreviated SVG.

SYSTEMATICS

Subfamily Crassispirinae McLean, 1971

Remarks: The characteristics common to members of this subfamily are the presence of a well developed parietal callus adjoining the anal sinus, a subsutural cord, sulcus with microscopic growth lines and occasionally with one or two spiral threads, a smooth protoconch with fine axials on about the last 0.25–0.5 whorl, and a teleoconch sculptured with axial ribs and spiral cords (McLean, 1971: 119). These characteristics are all present to a greater or lesser degree in genera within this large subfamily.

Genus *Buchema* Corea, 1934

Type Species: *Buchema tainoa* Corea, 1934, by original designation

Remarks: Corea (1934: 1–2) erected *Buchema* for *Carinodrillia*-like species that, among other differences, lacked a median carina on the nuclear whorls, had strong axial ribs with overriding heavy spiral cords, and with fine threads between the cords. In addition, she stated that *Buchema* have hair-like incremental lines that create a "cloth-like pattern, while their junction sometimes almost appears granulose." Not all species placed by subsequent workers in the genus have the spiral threads between cords, or visible growth lines, but the other characteristics are found consistently in the group members. The small *Buchema* are similar in appearance to the *Crassispira* subgenus *Monilispira* Bartsch and Rehder, 1939. They differ from the *Monilispira* in lacking beaded spiral cords on the whorl periphery and shell base. Plain cords, or cords with swellings on rib crests, not rounded beads, are present instead. Another distinguishing characteristic, although not unique to *Buchema*, is the location of the subsutural cord, which is usually very near the suture, not positioned well into the sulcus as in some of the other subgenera within *Crassispira*.

Buchema bellula (E.A. Smith, 1882)
(Figures 1–8)

Pleurotoma (*Clavus*) *bellula* E.A. Smith, 1882: 209–210.
Pleurotoma bellula E.A. Smith, 1882: Paetel (1888).
Drillia (*Clavus*) *bellula* (E.A. Smith, 1882): Tryon (1884: 191).
Buchema bellula (E.A. Smith, 1882): Maes (unpublished, from specimen labels ANSP 299773 and ANSP 297289, dated 9 Oct 1981); Williams (2006, 2009: number 3007, left, photographs of holotype only).
Not *Buchema bellula* (E.A. Smith, 1882): Williams (2005: number 3007, both photographs); Williams (2006, 2009: number 3007, right, 2 photographs only).
Sedilia melanacme (E.A. Smith, 1882): Fallon (2008: 12, 13, figs. 25a, b) (non E.A. Smith, 1882.)

Description: Shell 8.5 × 3.4 mm (holotype), fusiform, anterior portion truncated, consisting of ~8 whorls; color a faded pale yellow, except for the primary and secondary spiral cords, which are white to dingy white (Figure 1). Protoconch light brown, of 2 smooth whorls, bulbous but not wider than the first teleoconch whorl; tip partially immersed so that the first whorl is slightly tilted relative to the shell axis. Although not visible in the holotype because of wear, younger, less worn specimens, have fine axial riblets on the last 0.5 whorl (Figure 3). Teleoconch of ~6 whorls, whorls 4 and 5 with 7 primary and secondary cords: a subsutural cord, 3 secondary spiral cords in the sulcus, 2 primary cords on the whorls'

Figures 1–18. *Buchema* species. **1–8.** *Buchema bellula* (E.A. Smith, 1882), **1.** Holotype BM(NH) 1964223, St. Vincent, West Indies, 8.5 × 3.4 mm. Photo digitally enhanced (contrast and brightness) to show color pattern. **2.** ANSP 424360, Clifton Harbor, Union I., SVG, 8.1 × 3.4 mm. **3.** Same specimen as 2, enlarged views of protoconch. **4.** ANSP 424359, Corbec Bay, Canouan I., SVG, 8.9 × 3.6 mm. **5.** ANSP 355800, Grenada, 5.9 × 2.4 mm. **6.** ANSP 296638, E side of Prickly Pt., SW Grenada, 7.5 mm. **7.** ANSP 297289, mouth of St. George Harbor, W Grenada, 7.8 × 3.0 mm. **8.** USNM 1139712, Clifton Harbor, Union I., SVG, 8.9 × 3.5 mm. **9.** *Buchema melanacme* (E.A. Smith, 1882), holotype BM(NH) 1998116, St. Vincent, West Indies, 8.5 × 3.3 mm. **10.** *Buchema* aff. *bellula* (E.A. Smith, 1882), author's collection, Calliaqua Bay, St. Vincent I., SVG, 9.2 × 3.5 mm. **11–14.** *Buchema primula* (Melvill, 1923), **11.** Holotype BM(NH) 1982080, Cuba, 6.3 × 2.7 mm. Digitally enhanced as Figure 1. **12.** USNM 1139713, Annas Shoal, Grenada, 7.0 × 3.0 mm. **13.** ANSP 424362, E side of Prickly Pt., SW Grenada, 5.9 mm. **14.** Same specimen as 12, enlarged views of the protoconch. **Figures 15–17.** *Buchema nigra*, new species. **15.** Holotype USNM 1139714, Petit Nevis, SVG, 8.2 × 3.0 mm. **16.** Paratype, Peggy Williams coll., Man of War Bay, Tobago I., Trinidad and Tobago, 7.2 × 2.7 mm. **17.** Paratype ANSP 424361, Annas Shoal, Grenada, 8.1 × 3.0 mm. **18.** *Buchema* aff. *nigra*, author's collection, off Arraial do Cabo, Rio de Janeiro state, Brazil, 10.0 × 3.8 mm (missing protoconch).

periphery swollen at rib crests and appearing as rows of elongate beads, and 1 secondary cord below. Body whorl has an additional 4 secondary spiral cords on the shell base, and 4 more that encircle the anterior canal. Tightly packed spiral threads, ~3–10 in number, lie between the cords, the greater number between the cords of the body whorl where they are spaced further apart; 2 threads lie between the edge of the suture and subsutural cord on later whorls. Sulcus flat; sculpture as stated before with secondary spiral cords and threads; growth striae not readily evident, but faint where seen. Ribs number 10 on the penultimate and 8 to the varix on the body whorl, very short, only obvious at the whorl periphery, reduced to slight swellings above and below the peripheral cords. Aperture widest medially; anal sinus deep and rounded posteriorly, but not constricted at the entrance, or only very slightly so in mature specimens. Varix a distinct hump behind the anal sinus; outer lip thin with 2 irregular narrow axials near its edge, and scalloped by the ends of spiral cords; with a shallow stromboid notch. Inner lip thin, lies along the columella and parietal wall; a callus at its junction with the outer lip forms the parietal wall side of the anal sinus.

Type: Holotype BM(NH) 1964223.

Type locality: St. Vincent, West Indies.

Other Material Examined: Four spec., worn, at 30 ft [9.1 m] on sand, shell and coral, 1/8 mi [0.2 km] W of Ft. George, St. George, Grenada, (ANSP 296915); 3 spec., 5.7, 7.5, and 8.2 mm (broken tip), at 0–0.9 m, in *Thalassia*, sand coral rock, E side of Prickly Pt., SW Grenada, coll. by R. Ostheimer, Jan–Feb 1964 (ANSP 296638); 1 spec., 5.9 × 2.4 mm, Grenada, coll. by Cosman (ANSP 355800); 1 spec., 7.8 × 3.0 mm, at 7.3–11.0 m, trash, coral rubble, mud, mouth of St. George Harbor, W. Grenada (ANSP 297289); 1 spec., 2.6 mm juvenile, at 7.3 m, in sand, fine grass, 500 yds [457 m] off fish market, W of St. George, Grenada, coll. by R. Ostheimer, 12 Feb 1964 (ANSP 299787); 1 spec., 4.6 mm juvenile, at 3.7 m, in sand, mud, coral rubble, lagoon channel, St. George Harbor, Grenada, coll. by R. Ostheimer, 8 Jan 1964 (ANSP 297412); 1 spec., 7.9 × 3.0 mm, at 12.2–15.2 m, Carriacou I., Grenada, coll. by T. McCleery May 2004 (author's coll.); 6 spec., 8.7 × 3.5, 9.0 × 3.7 (both USNM 1139710), 8.6 × 3.3 (BMSM 17964), 6.7 × 2.9, 6.2 × 2.5 (both UF 441321), and 8.9 × 3.6 mm (ANSP 424359), at 7.6 m, on rock and sand, Corbec Bay, Canouan I., SVG, coll. by G. Mackintosh 8, 9 Jun 2004; 15 spec., 8.1 × 3.4 (ANSP 424360), 8.3 × 3.5, 6.7 × 2.8 (both USNM 1139711), 8.8 × 3.6, 6.5 × 2.8 (both UF 441320), 6.5 × 2.9, 5.9 × 2.7 (both BMSM 17965), 6.1 × 2.6, 5.7 × 2.5 (both P. Williams coll.), 6.7 × 2.9, 6.1 × 2.6, 7.8 × 3.2, 8.8 × 3.7, 6.3 × 2.7 and 7.8 × 3.5 mm (missing protoconch, anthor's coll.), at 10.7 m, Clifton Harbor, Union I., SVG, coll. by G. Mackintosh 30 May 2004; 7 spec. 9.9 × 4.0, 9.2 × 3.5, 9.3 × 3.9, 9.6 × 3.8, 8.2 × 3.5 (broken apex), 6.0 × 2.4, and 5.8 × 2.5 mm, at 10.7 m, Chatham Bay, Union I., SVG, coll. by G. Mackintosh, 8 Apr 2007 (author's coll.); 1 spec., 11.1 × 4.5 mm, at 8 m, Green I., Grenada, coll. by G. Mackintosh, 1 Nov 2003 (author's coll.); 1 spec., 7.4 × 2.9 mm, at 10.7 m, Saline I., Grenada, coll. by G. Mackintosh, 1 Feb 1997 (author's coll.); and 1 spec., 8.9 × 3.5 mm (USNM 1139712), and 207 others, intertidal, crabbed, Clifton Harbor, Union I., SVG, coll by P. Fallon, 16 Jun 2007 (author's collection).

Distribution: SVG (Canouan I., Union I.) and Grenada (Grenada I., Carriacou I., Green I., Saline I.).

Remarks: This species clearly has the characteristics of *Buchema*, with heavy spiral cords overriding the ribs and spiral threads in between. It is virtually unknown because the original description by Smith in 1882 was not illustrated, and until now this remained the only description of the species. Virginia O. Maes identified several lots in the ANSP collected in Grenada as this species, and she was likely the first to place it in the genus *Buchema*, (unpublished, based on information from specimen labels ANSP 299773 and ANSP 297289, dated 9 Oct 1981). Williams (2006: number 3007) was the first to publish a photograph of the holotype.

The largest specimen examined had a length of 11.1 mm. Color seems to vary among local populations; shallow water specimens taken on Union I., SVG, are brown (Figure 8), while gold-colored specimens, probably the holotype's original color, have been found at 10.7 m in Clifton Harbor, also Union I. (Figure 2). The black form has been taken at 5.5–7.6 m in Chatham Bay, Union I., at Canouan I., SVG (Figure 4), and from Grenada at unknown depth (Figure 5). None of these color forms have been found to have differences that might suggest a separate species.

Other characters are variable in *B. bellula*. The number of ribs and spiral cords vary from 10 to 12 ribs and 5 to 10 spiral cords on the penultimate whorl among the specimens examined. There can be as few as 1 or as many as 4 primary cords (Grenadian specimens (Figures 6 and 7). Shallow water Union I. specimens were quite uniform in having 2 (Figure 8). The number of spirals on the last whorl varies from 13 to 25.

Buchema bellula is easily recognized by the regularly spaced, smooth, fine light-colored spiral cords (the secondary spirals) spaced along the entire length of the shell, and by the 1–4 primary white cords swollen at the crests of broad, short ribs that are mostly limited to the whorls periphery. It is most similar to *Buchema primula* (Melvill, 1923); see the remarks under that species for differences. *Buchema melanacme* (E.A. Smith, 1882) differs in having an excavated sulcus with well-marked growth striae and without secondary spiral cords, longer and more distinct ribs, and broken or slightly nodulose spirals on its base (Figure 9). Also, *B. melanacme* has patches of darker color between ribs, which contrasts with *B. bellula*'s uniform base color. *B. nigra*, new species is similar to the black form of *B. bellula*—see under *B. nigra* for a discussion of their differences.

An undescribed species, shown in Figure 10 and temporarily identified as *Buchema* aff. *bellula*, is larger, peripheral spirals only slightly swollen, and secondary spirals in the sulcus are lacking.

Buchema primula (Melvill, 1923)
(Figures 11–14)

Drillia primula Melvill, 1923: 166, pl. 4, fig. 9: Trew (1987: 58).
Buchema primula (Melvill, 1923): Williams (2005, 2006, 2009: number 3013).
Buchema bellula (E.A. Smith, 1882): Williams (2005, 2006, 2009: number 3007, only second photograph from right) (non E.A. Smith, 1882).

Description: Shell 6.3 × 2.7 mm (holotype), with ~7 whorls; fusiform, stout, anterior end truncated (Figure 11). Protoconch of ~2 worn whorls. On the fresh specimen shown in Figure 12, there are 1.5 regularly expanding, symmetrical, smooth whorls, followed by 0.5 whorl with 6 distinct, prominent, curved riblets; protoconch white on the holotype, light brown with a dark brown band next to the suture on the fresh specimen (Figure 14). Spiral sculpture consists of a subsutural and 3 other cords on the spire whorls, 2 swollen at the rib crests. Body whorl has 4 additional spiral cords on shell base, also swollen at the rib crests, and 4 plain spiral cords on the anterior canal. On the fresh specimen, the subsutural cord is offset from the suture by 1–3 distinct, packed spiral threads, and undulates with ribs that underlie the appressed suture. Spiral threads are present between the cords overall. Sulcus moderately wide, slightly excavated, with spiral threads throughout. Axial sculpture of 11 ribs on the penultimate and 9 to the varix on body whorl, where they evanesce on the shell base. Ribs about as broad as their interspaces. Outer lip broken on holotype; on fresh specimen lip thin, slightly scalloped by 8 spiral cords; weak stromboid notch present; anal sinus lies just below the subsutural cord, deep and rounded at its apex, sides slightly divergent. Varix lies behind the anal sinus, about the width of two swollen ribs. Inner lip thin, transparent, with a parietal lobe at its junction with the outer lip. Aperture narrow, ending in a short, open anterior canal. Shell color pale yellow, probably faded; fresh specimens examined are all dark brown, lighter near apex, with a white band spiral cords on the periphery.

Holotype: Holotype BM(NH) 1982080.

Type Locality: Cuba.

Other Material Examined: 1 spec., 7.0 × 3.0 mm, at 12 m, Annas Shoal, Grenada (USNM 1139713); 1 spec., 5.9 mm, at 0–0.9 m, in *Thalassia*, sand, coral rock, E side of Prickly Point, SW Grenada, coll. by R. Osthcimer (ANSP 424362); 1 spec., 6.6 × 2.5 mm, at 0.3–0.9 m, Prickly Bay, SW Grenada (ANSP 299773); 1 spec., 6.5 × 2.6 mm, from on coralline sand among dead coral at 11 m, Saline I., Grenada, coll. by G. Mackintosh, Feb 1997 (UF 441322); and 1 spec., 7.4 × 2.9 mm, on rock and sand at 7.6 m, Corbec Bay, Canouan I., SVG, coll. by G. Mackintosh, 8 Jun 2004 (BMSM 17966); 2 spec., 7.7 × 3.1 and 6.8 × 2.9 mm, at 5.5 m on silt-covered rocks, Corbec Bay, Canouan I., SVG, coll. by G. Mackintosh, 6 Dec 2006 (author's coll.).

Distribution: Unspecified type locality in Cuba; examined specimens are limited to SVG (Canouan I.) and Grenada (Saline I.). A specimen in Peggy Williams collection not examined (Williams, 2005: number 3007, second photo from right), is 6.5 × 2.5 mm, and was taken at 9 m, Canoe Bay, Grenada, coll. by G. Mackintosh, 20 Sep 1996 (Tippett, pers. observ.).

Remarks: *Buchema primula* has spiral cords overriding relatively broad ribs, with spiral threads in between the cords, characteristics of the genus. Intraspecific variation is seen in the number and degree of swelling of the peripheral white cords, and the whiteness of the cords. Cords are more swollen in the specimen depicted in Figure 12 than the one shown in Figure 13. Another specimen not shown, ANSP 299773, has only two white peripheral cords.

This species is most similar to and has been mistaken for *B. bellula* (Williams, 2005, 2006, 2009: number 3007, second photo from right). The confusion with *B. bellula* is understandable; only Smith's description has been available for study, and only recently has a photograph of the holotype of *B. bellula* been published (in Williams, 2006, 2009: number 3007, left photos). *Buchema bellula* has a different protoconch: dark glassy brown, almost black, of 2 smooth whorls, bulbous but not wider than the first teleoconch whorl, and with tip partially immersed so that the first whorl is slightly tilted relative to the shell's axis. This contrasts with the 2 regularly expanding, symmetrical, and smooth whorls of *B. primula* that bear axial riblets terminally (Figure 14). The teleoconch sculpture differs too. *B. primula* has a thicker subsutural cord, which undulates with the ribs that underlie the appressed suture; a narrower sulcus; typically 3 peripheral spiral cords (not 2) that are swollen where they cross the ribs, the swellings rounder or shorter, and the ribs narrower, with the interspaces about the same width; more pronounced and longer ribs on the body whorl; and fewer spiral cords on the body whorl.

Buchema nigra new species
(Figures 15–17)

Buchema bellula (E.A. Smith, 1882): Williams (2005, 2006, 2009: number 3007, rightmost photograph) (non E.A. Smith, 1882).

Description: Shell 8.2 × 3.0 mm (holotype), narrowly fusiform, truncated anteriorly; 7.5 whorls (Figure 15). Protoconch of 2.5 smooth glassy whorls, except the last 0.25 whorl with ~4 faint axial riblets; whorls dark brown, lighter mid-whorl. Teleoconch of 5 whorls; first whorl with 4 spiral cords, uppermost a subsutural cord slightly thicker than the second, third

is swollen where it overrides the ribs and forms the periphery of the shell, fourth lies next to the suture with the succeeding whorl and is very fine. Spiral cords increase to 6 on the penultimate whorl, the 3 peripheral ones are slightly swollen across the ribs. Subsutural cord heaviest and 2 in the sulcus, which is flat. Body whorl has a total of 15 spiral cords: 6 to the suture line as in the penultimate whorl, 4 more on shell base that are slightly swollen across the ribs, and 5 encircle the anterior canal. Distinct spiral threads are packed between the spiral cords, from about the third teleoconch whorl to the anterior canal. Ribs begin about midway in the sulcus and evanesce on shell base; number 11 to the varix on body whorl, 12 on penultimate; distance between the ribs less than the rib width. Varix lies close to the edge of the outer lip, just behind the anal sinus, and is broader and higher than the ribs. Outer lip thin, scalloped by the ends of spiral cords, and with a slight stromboid notch. Anal sinus u-shaped, shallow, slightly constricted on parietal side by callus; located just below subsutural cord. Inner lip narrow, appressed to the columella and parietal wall, terminating posteriorly at the parietal callus that forms the roof of the aperture. Aperture ovate, about 37% of the overall height of the shell, including the anterior canal, which is very short. Shell color very dark brown to black, spiral threads between the two peripheral cords, and between subsutural cord and suture are dark brown to black; spiral cords whitish; subsutural cord brown.

Types: Holotype USNM 1139714. Paratypes: 1 spec., 7.9 × 2.9 mm, at 40–50 m, Carriacou I., Grenada, coll. by T. McCleery, May 2004 (UF 441323); 1 spec., 7.2 × 2.8 mm, at 9.8 m, Petit Nevis, SVG, coll. by G. Mackintosh, 19 Aug 2000 (BMSM 17967); 1 spec., 7.4 × 3.2 mm, at 12.2 m, S end of Baliceaux I., SVG, coll. by G. Mackintosh, April 1997 (USNM 1139715); 1 spec., 8.1 × 3.0 mm, at 13.7 m, Annas Shoal, St. George, Grenada, coll. by G. Mackintosh, 4 Aug 1996 (ANSP 424361); 1 spec., 7.2 × 2.7 mm, at 3.7 m under rock, Man of War Bay, Tobago I., Trinidad and Tobago, coll. by G. Mackintosh, 11 Feb 1998 (P. Williams coll.).

Type Locality: Petit Nevis, St. Vincent and the Grenadines, in 8.5 m.

Distribution: SVG (Baliceaux I.; Petit Nevis); Grenada (Grenada I.; Carriacou I.); and Trinidad and Tobago (Tobago I.).

Remarks: This species has the characteristics of the genus *Buchema*, with spiral cords overriding relatively broad ribs, and spiral threads in between the cords. *B. nigra* is most similar to the black form of *B. bellula*, but its peripheral cords are less swollen on the rib crests, and it has a brown subsutural cord, which is white in *B. bellula*.

Unlike *B. bellula*, little variation is seen in specimens of *B. nigra* from different localities within its known range. The specimen from Man of War Bay, Tobago (Figure 16) is indistinguishable from the holotype (Petit Nevis, SVG), as is the specimen from Grenada (Figure 17). An undescribed species from off Arraial do Cabo, Rio de Janeiro state, Brazil (Figure 18), has similar sculpture but is larger and brown in color. Only this single imperfect specimen was available, so no further analysis was undertaken. The right-most photo in Williams (2009: number 4014), which is also from Brazil, may be this undescribed species.

Etymology: From the Latin adjective *niger*, meaning black (Oxford Latin Dictionary). This species is named for its characteristic color, which is a very dark brown to black in strong light under magnification, but decidedly black to the naked eye.

Genus *Miraclathurella* Woodring, 1928

Type Species: *Miraclathurella vittata* Woodring, 1928, by original designation. Miocene of Jamaica (Bowden Formation).

Remarks: Woodring (1928: 189) described members of this genus as being very slender, having 2.5–3.0 stout nuclear whorls with a few opisthocline axial riblets, a teleoconch with narrow, closely spaced axial ribs, narrow and more closely spaced on body whorl, overridden by strong spiral cords, and a sulcus with a strong subsutural cord. In addition they have a deep, round anal sinus, very long and narrow aperture, relatively long anterior canal, and a deep or relatively deep stromboid notch. The combination of characters that separate this group from both *Buchema* and *Crassispira* is a slender shell, narrow aperture, a relatively heavy varix close to the edge of the outer lip, a relatively long anterior canal, and a strong stromboid notch.

Miraclathurella peggywilliamsae new species
(Figures 19–22)

Miraclathurella ? .—Williams, 2005: number 9036.

Description: Shell with 8 slightly convex whorls (holotype), 10.3 × 3.6 mm, fusiform, slender, spire about 58% of overall shell height (Figure 19). Protoconch paucispiral, ~1.75 smooth whorls, except last 0.25 whorl with 4 fine axials; tip partially immersed, giving the shell apex the appearance of being flat-topped. The transition to the teleoconch is marked by the appearance of the subsutural cord and angular axial ribs. Teleoconch of 6.25 whorls bearing 3–5 spiral cords that are beaded at the intersection of axials on early whorls, becoming more elongated and less swollen on the body whorl, and then plain cords on the varix and outer lip. Four more beaded cords are present on the shell base; anterior canal with 8 rather plain spiral cords. Sulcus about a third the height of the whorl, slightly excavated, marked with arcuate incremental growth lines. Subsutural cord distinct, smooth, and located very close to the suture except on the last 2 whorls where it is slightly offset below. Finely granulose spiral threads, spaced about as far apart

as they are wide and variable in thickness, are present between the cords, in the sulcus, and a few between the subsutural cord and the summit of the last 2 whorls only. Axial ribs present but reduced in the anterior half of the sulcus, continue to shell base where they evanesce. Axial ribs are narrow with wide interspaces in early whorls, and low and broad with narrow interspaces on later whorls. Penultimate whorl has 23 axials; body whorl about 18 to the varix. Varix a thick swelling a short distance behind the edge of the outer lip. Outer lip thin and straight, running from the anal sinus to the small but distinct stromboid notch. A short axial is present near edge of outer lip. Anal sinus deep, its apex round, opening partially constricted by the parietal callus and projection of the outer lip. Aperture oval, joins a distinct, open anterior canal, which begins at the constriction imposed by the stromboid notch. Canal turned slightly to the right, viewed ventrally. Inner lip narrow, appressed to the columella and parietal wall its entire length. Roof of the aperture formed by the parietal callus that fills the junction of the inner and outer lips. Shell color a light golden yellow; 2 peripheral cords lighter still, almost white.

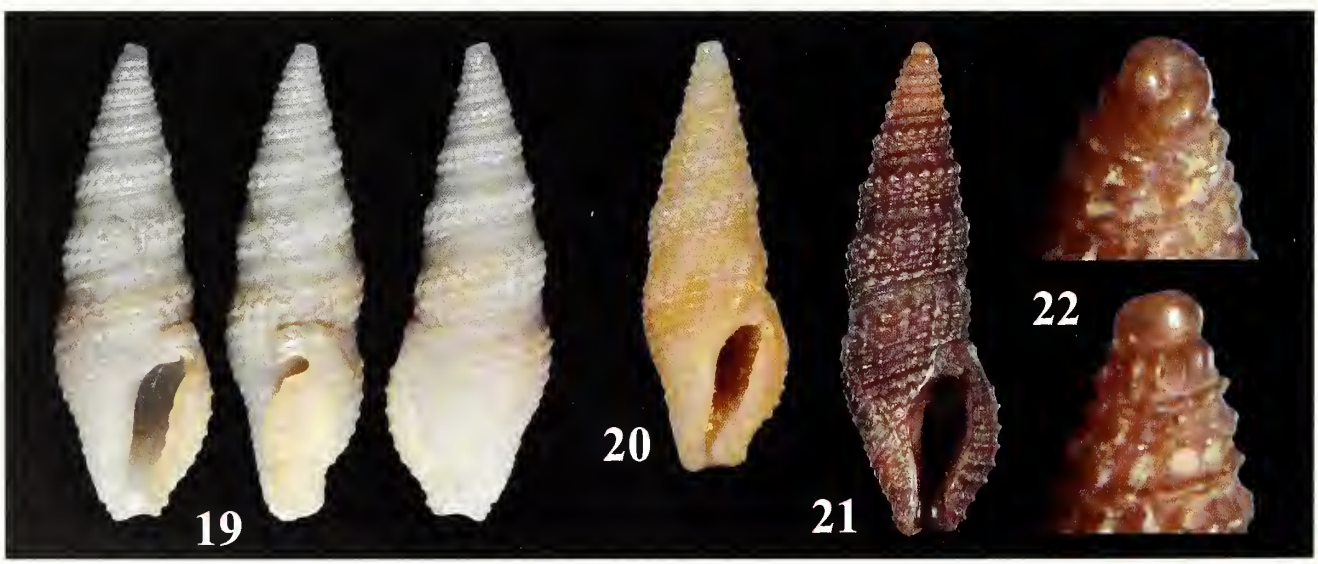
Types: Holotype USNM 1139716; Paratypes: 1 spec., 9.8 × 3.3 mm, at 7.6 m, St. Elair Pt., Friendship Bay, Bequia, SVG, coll. by G. Mackintosh, 30 Jul 1996 (UF 441324); 4 spec., 10.3 × 3.5, 10.1 × 3.7, 10.4 × 3.5 (missing protoconch), and 9.9 × 3.3 mm, at 12.2 m, S end of Baliceaux I., SVG, coll. by G. Mackintosh, 25 Apr 1997 (ANSP 424358); 1 spec., 9.7 × 3.5 mm, at 12.2 m, S end of Baliceaux I., SVG, coll. by G. Mackintosh, 23 Apr 1997 (BMSM 17968); 2 spec., 9.9 × 3.6 (missing protoconch) and 8.3 × 2.7 mm, at 10.7 m, Baliceaux I., SVG, coll. by G. Mackintosh, 24 Apr 1997 (P. Williams coll.); 1 spec., 9.2 × 3.1 mm, at 3.0 m, Glover I., Grenada, coll. by G. Mackintosh, 26 Nov 1996 (ANSP 424356); 1 spec., 10.2 × 3.8 mm (missing apex), at 6.7 m, Glover I., Grenada, coll. by G. Mackintosh, 4 Nov 1996 (P. Williams coll.); 1 spec., 9.4 × 3.5 mm (missing apex), at 9.1 m, Devil's Bay, Grenada, coll. by G. Mackintosh, 8 Sep 1996 (P. Williams coll.); and 1 spec., 10.6 × 3.5 mm, at 12.8 m, Limekiln Bay, Carriacou, Grenada, coll. by G. Mackintosh, 28 Jun 1998 (BMSM 17969).

Type Locality: Baliceaux Island, St. Vincent and the Grenadines, at 12.2 m depth.

Other Material Examined: 1 spec., 9.3 × 3.4 mm (missing apex), Clifton Harbor, Union I., SVG, coll. by P. Fallon (author's coll.); 1 spec., 10.6 × 3.5 mm, at 3.7 m under rock, Man of War Bay, Tobago I., Trinidad and Tobago, coll. by G. Mackintosh, 2 Nov 1998 (ANSP 424357); 1 spec., 8.9 × 3.0 mm, at 9.1 m, Parlatuvier Bay, Tobago I., Trinidad and Tobago, coll. by G. Mackintosh, 14 Oct 1998 (USNM 1139718); 1 spec., 10.1 × 3.5 mm, at 6.1 m, Pampatar, Margarita I., Venezuela, coll. by G. Mackintosh, 15 Jun 1993 (USNM 1139717).

Distribution: SVG (Bequia I., Baliceaux I., Union I.); Grenada (Grenada I., Glover I., Carriacou I.); Trinidad and Tobago (Tobago I.); and Venezuela (Margarita I.).

Remarks: The genus was erected for fossil species of the Bowden Formation of Jamaica (Woodring, 1928), and although very similar, there are some minor differences from Woodring's description of the genus. The nuclear whorls number 1.75, not 2.5–3.0, although there is some room for difference in interpretation, and the anterior canal appears relatively shorter than those of the fossil specimens placed in this genus. The shell's



Figures 19–22. *Muraclathurella peggywilliamsae* new species. **19.** Holotype, USNM 1139716, Baliceaux I., SVG, 10.3 × 3.6 mm. **20.** Paratype, ANSP 424356, Glover I., Grenada, 9.2 × 3.1 mm. **21.** ANSP 424357, Man of War Bay, Tobago I., Trinidad and Tobago, 10.6 × 3.5 mm. **22.** Same specimen as 21, expanded views of the protoconch.

spindle shape, elongate aperture, prominent varix close to the outer lip, distinct stromboid notch, subsutural cord and other sculptural details support placement here, as they are consistent with his description. The height of this species falls within the range of 6.9–15.5 mm reported for Bowden Formation fossils (Woodring, 1928: 190–191). The largest specimen of *M. peggywilliamsae* examined is 12.6 × 3.8 mm, but is not included in the list of examined specimens above because the locality data has been lost. The only other extant species from the TNWA area (tentatively placed in the *Miraclathurella* by the describer) is *M. clendenini* García, 2008, the largest of which was reported to be 10.1 mm (García, 2008: 11).

Geographic variation is evident in specimens examined. Those from St. Vincent and the Grenadines are light golden yellow, the Grenadian ones a darker golden color (Figure 20), and those from Tobago and Margarita I. mostly brown (Figure 21). The Man of War Bay, Tobago specimen has fewer cords on the body whorl and anterior canal, the spiral sculpture is more pronounced, the beading is slightly larger, the axials better defined, and the elongated beads on the body whorl do not tend to coalesce into a thick cord. The Margarita I. specimen is similar to the holotype in most respects except that it has fewer threads between the cords. Although only minor differences in sculptural detail are present in the specimens from these more distant geographic areas (from the type locality), they have been left out of the type series. However, it is not believed they warrant separation at the specific level because of these differences.

Darrylia kleinrosa (Usticke, 1969) is closest to this but differs in being pink in color, generally smaller, and in lacking a distinctive subsutural cord. It also has a strong denticle at the beginning of the anterior canal that constricts its opening (García, 2008: 10). *Crassispira nigrescens* (C. B. Adams, 1845) has a similar appearance but, most significantly, it has a much shorter aperture and anterior canal, and only a modest varix, compared with the longer anterior canal and thick varix of *M. peggywilliamsae*. Also, the beading on *C. nigrescens* is generally heavier.

Etymology: Named after Peggy Williams because of her passion for tropical western Atlantic turrids and promotion of their greater understanding with her book, *Shallow-Water Turridae of Florida and the Caribbean*, and for recognizing this species as undescribed.

ACKNOWLEDGMENTS

I wish to thank Dr. Jon Greenlaw who first interested me in the review of malacological literature for what it could reveal about the kinds, habitat and distribution of mollusks of the TNWA, and for his helpful suggestions on the manuscript. I am grateful to Dr. Donn Tippett who generously gave so much of his time to explain the complex world of turrid systematics, terminology, for his advice and opinion on the manuscript, and very importantly, use of his invaluable turrid study notes. Thanks are due Dr. Jerry Harasewych and Paul Callomon, curators of the USNM and ANSP malacology departments, respectively, who allowed me free run of the valuable collections under their care. I also thank Peggy Williams for generously parting with many of the Mackintosh crassispirine turrids, and for her astute observations helpful in this research, and also to Randy Allamand and Andre Poremski, both for supplying additional shells collected by the Mackintoshes. Acknowledgement is due Gary and Margaret Mackintosh because, were it not for the years of sailing and collecting around the Caribbean, these new species would have remained unknown, and we would be ignorant of the surprising diversity of small crassispirines in the southeastern Caribbean. Gary's many dives and the resulting mass of material collected from relatively inaccessible corners of the Caribbean have not been matched by any other modern day explorer.

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A new species of *Cerberilla* (Gastropoda: Nudibranchia: Aeolidiidae) from northeastern Brazil

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ABSTRACT

Few specimens of the 15 named species of *Cerberilla* are known. Body color pattern and teeth morphology have been used as the main diagnostic characters to separate species of the genus. To date, *Cerberilla tanna* is the only species of the genus described from the western Atlantic. Because its original description does not provide much information about body coloration, the identity of this species remained unclear until now. In this paper, we describe *Cerberilla potiguara*, a new species from the northeastern coast of Brazil, and compare it with *C. tanna*. The holotype of *C. tanna* was located and examined. *Cerberilla potiguara* new species is longer than *C. tanna* but has relatively shorter oral tentacles and a narrower foot; the radular teeth of *Cerberilla potiguara* new species have prominent central and marginal cusps, which are absent in *C. tanna*. A prominent unarmed penis associated with a conical atrium, observed in *Cerberilla potiguara* new species and other *Cerberilla* species, is herein considered a distinguishing characteristic of the genus among the Aeolidiidae.

Additional keywords: Biodiversity, Opisthobranchia, Rio Grande do Norte, morphology, Marcus collection.

INTRODUCTION

Because of their habit of burrowing in sand, few specimens are known of the 15 named species of *Cerberilla*. Body color pattern and teeth morphology have been used as the main diagnostic characters to separate the species (McDonald and Nybakken, 1975; Hermosillo and Valdés, 2007). In fact, body color and its patterns constitute an important character for taxonomic studies of nudibranchs in general (Behrens, 2005). Only recently the nudibranch fauna from the western Atlantic began to be well illustrated, with the publication of books containing color photographs of a series of species (Redfern, 2001; Valdés et al., 2006; García-García et al., 2008). Previously, most western Atlantic species were known only from black-and-white ink drawings and generally brief descriptions of color (e.g. Marcus, 1955, 1957). In addition, some original descriptions of western Atlantic species were based on preserved and faded specimens (e.g. *Nanuca sebastiani* Marcus, 1957), the color of original living forms remained unknown.

The only named species of *Cerberilla* known from the western Atlantic is *Cerberilla tanna* Marcus and Marcus, 1960 described from a single preserved specimen from Texas, USA. The only mention of body color in the original description was of the presence of an "orange-brown spot on the outer surface of many, not all, cerata" on the dirty-yellow preserved holotype (Marcus and Marcus, 1960). Since the original description, new specimens of *C. tanna* have not been studied and this species remained for a long time as the only known representative of the genus in the western Atlantic. Humann and Deloach (2002) illustrated a brilliant blue *Cerberilla* from St. Vincent Island, called *Cerberilla* sp., in their book on reef creatures. This morphotype was also photographed in Florida, Bahamas, and Bonaire (Behrens, 2003; Hutchinson, 2003; Ferretti, 2009). Later, a pale-cream *Cerberilla* was recorded in the Gulf of Mexico (Hooper, 2004) and subsequently photographed from the coast of Mississippi and St. Vincent Island (Perry, 2005; Wilk, 2005). Another pale-cream morphotype, from Florida, was illustrated by Ianniello (2003) and Valdés et al. (2006: 276–277, as *C. tanna*). These pale-cream morphotypes have cerata with dark spots, more closely resembling the characteristics of *C. tanna*. However, the identity of all morphotypes, the brilliant blue and the two pale-cream forms, remained unclear because no data on their anatomy were available.

Material of the blue *Cerberilla*, recently collected on the northeastern coast of Brazil, is described herein. We compare it with the type material and the original description of *C. tanna*. A new species is described, and the situation of the genus in the western Atlantic is, at least in part, clarified.

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MATERIALS AND METHODS

The holotype of *Cerberilla tanna* new species was located in the Marcus collection, deposited in the Malacological collection of the Museu de Zoologia da Universidade de São Paulo (MZSP), Brazil. Living material of the new species was photographed *in situ*, manually collected, fixed with 4% formalin, and preserved in 70% ethanol. It was deposited in the Malacological collection of the Museu Nacional/Universidade Federal do Rio de Janeiro (MNRJ), Brazil. Specimens were observed using a binocular microscope. External structures of interest were photographed using a Nikon digital camera coupled to the microscope. Material of the new species was dissected through a dorsal incision. The buccal mass was removed and placed in 10% sodium hydroxide until the jaws and radula were isolated from the adjacent tissue. The jaws and radula were then rinsed in water, dried, and mounted for examination with a scanning electron microscope (SEM). The reproductive system was drawn using the camera lucida mounted on the binocular microscope. The holotype of *C. tanna*, previously dissected, was photographed, but, in order to preserve its morphology, no new cuts or dissections were made.

SYSTEMATICS

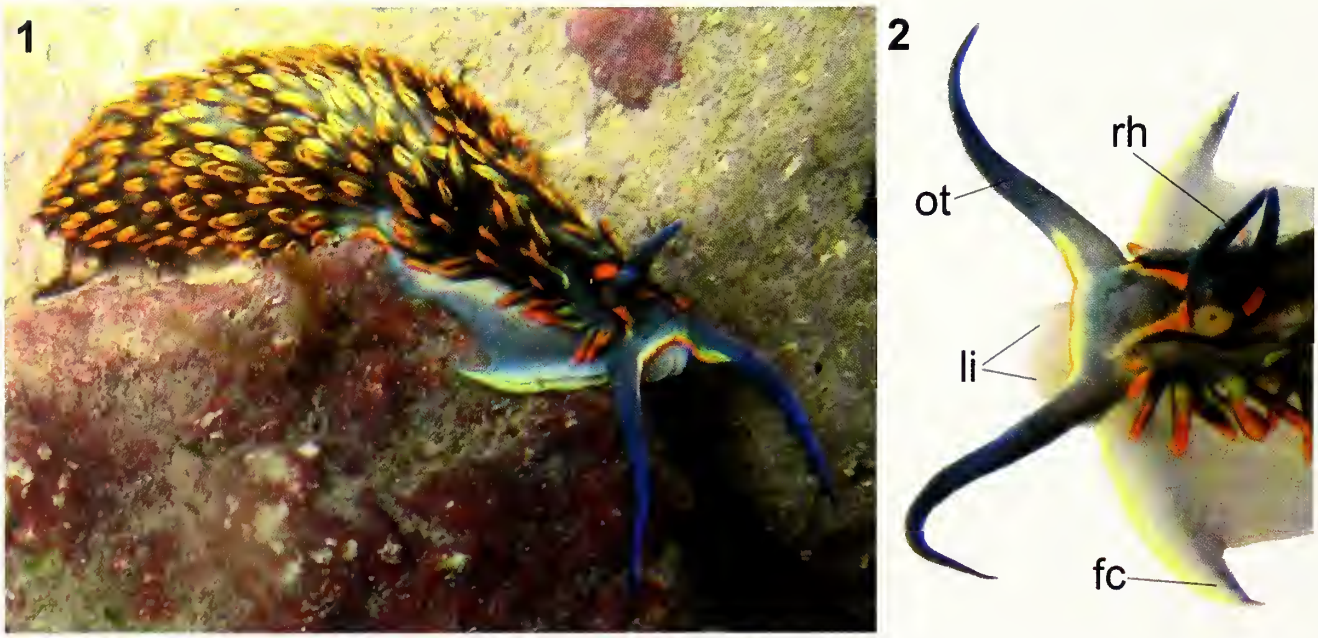
Family Aeolidiidae Gray, 1827
Genus *Cerberilla* Bergh, 1873

Cerberilla potiguara new species
(Figures 1–6, 10)

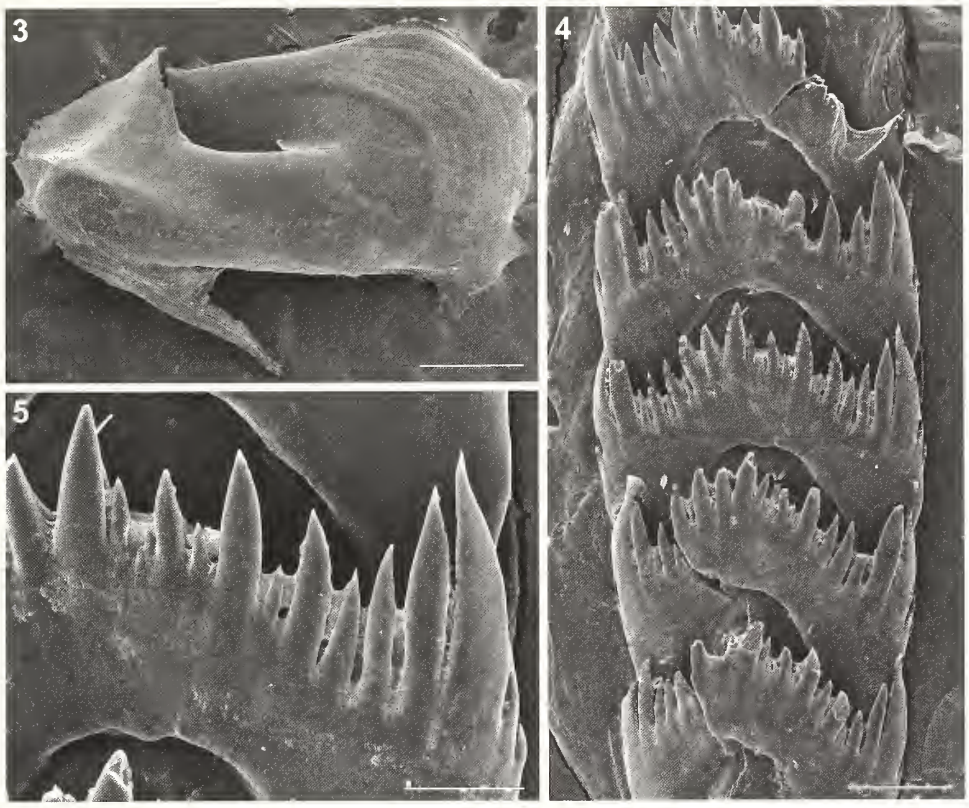
Cerberilla sp. Humann and Deloaeh, 2002: 309; Valdés et al. 2006: 276–277.
Cerberilla sp. 7.—Rudman, 2004.
Cerberilla tanna.—Behrens, 2003.

External Morphology (Figures 1, 2, 10): Living holotype 45 mm long (18 mm long preserved). Body long, narrow. Distinct head, cylindrical oral tentacles and rhinophores. Pair of rounded, slightly protruded lips. Oral tentacles relatively short (3 mm long, preserved), projected laterally. Rhinophores short, smooth, with adjacent bases. Small eyes located at base of each rhinophore, laterally on head. Foot wider than body, with triangular anterior corners; anterior margin broader, tapers slightly, rounded posterior end. Cerata club-shaped, 15 rows, anterior rows more spaced; posterior cerata longer (8 mm long, preserved) covering dorsum. Gonopore, body right side, below first row of cerata. Anal and renal openings, body right side, behind pericardium, between fifth and sixth cerata rows.

Coloration (Figures 1, 2): Body brilliant blue. Upper oral region with orange line bordered in yellow, extended to inner area of each oral tentacle base. Oral tentacles blue. Oral lips light blue. Foot anterior margin yellow bordered. Rhinophores blue. Eyes region less pigmented. Head with remarkable pattern: thin triangular orange spot in front of each rhinophore; black line borders external side of each triangular spot, runs toward pericardium and behind rhinophores, where borders elliptical orange spot. Pericardial zone grayish black. Cerata grayish-blue, anterior portion with round yellow-



Figures 1–2. *Cerberilla potiguara* new speeies, living holotype (MNRJ 15111, length: 45 mm). **1.** Speeimen erawling near reef. **2.** Detail of structures of the anterior region of the body. Abbreviations: **fc,** foot corner; **li,** lips; **ot,** oral tentacle; **rh,** rhinophore. Photo: Liana Mendes.



Figures 3–4. *Cerberilla potiguara* new species, holotype (MNRJ 15111), scanning electron micrographs. **3.** Left jaw, external face. Scale bar = 500 µm. **4.** Radular teeth, general view. Scale bar = 100 µm **5.** Detail of the denticles of the eighth tooth. Scale bar = 50 µm.

orange spot; spot longer on anterior cerata; posterior cerata with spot located near apical zone.

Radula and Jaw (Figures 3–5): Uniseriate radula, 19 teeth (holotype, 45 mm long alive). Radular teeth large, many times as wide as long. Tooth with series of denticles of different sizes (around 25 per tooth), submarginals highest; in some teeth, each short denticle alternates with high denticle; sequence of up to three high denticles located near central region of tooth. Jaw plates wide, rounded, slightly larger in posterior region; smooth projecting masticatory border.

Reproductive System (Figure 6): Hermaphroditic duct long, narrow. Ampulla very long, flattened, with four folds proximally; distal portion narrow, connected to prostate as well as to common atrium with vagina and receptaculum seminis insertion. Receptaculum seminis heart-shaped, projecting in a thin tube. Prostate voluminous, curved. Deferent duct large, curved. Penis large, unarmed. Male atrium conical, with small oval aperture.

Holotype: MNRJ 15111, Liana Mendes and Aline S. Martinez col., 14 Nov. 2008.

Type Locality: Praia de Búzios, Rio Grande do Norte, northeastern coast of Brazil (06° 00′13″ S; 35°06′24″ W), intertidal zone of the coastal reef.

Etymology: The specific name refers to the Potiguar native Brazilian people, who inhabited the region of Rio Grande do Norte, Brazil.

Geographic Distribution: Known from type locality, Florida, the Bahamas, St. Vincent and the Grenadines, and Bonaire (Humann and Deloach, 2002; Behrens, 2003; Rudman, 2004; Valdés et al. 2006).

Cerberilla tanna Marcus and Marcus, 1960
(Figures 7–9)

Cerberilla tanna Marcus and Marcus, 1960: 259, figures 18–19.
?*Cerberilla tanna*.—Hooper, 2004; Perry, 2005; Wilk, 2005.
?*Cerberilla tanna*.—Ianiello, 2003; Valdés et al., 2006: 276.

External Morphology (Figures 7–9): Strongly contracted and curved holotype, 14 mm long. Body long, narrow. Distinct head with cylindrical oral tentacles and rhinophores. Oral region with marginal, grooved lip. Oral tentacles long (5 mm), projecting laterally. Rhinophores very short, smooth, with adjacent bases. Foot wider than body, oval shape, central region larger than the rest, triangular anterior corners. Cerata club-shaped, 13 closely set rows; anterior rows more spaced; posterior cerata longer (5 mm long, preserved) covering

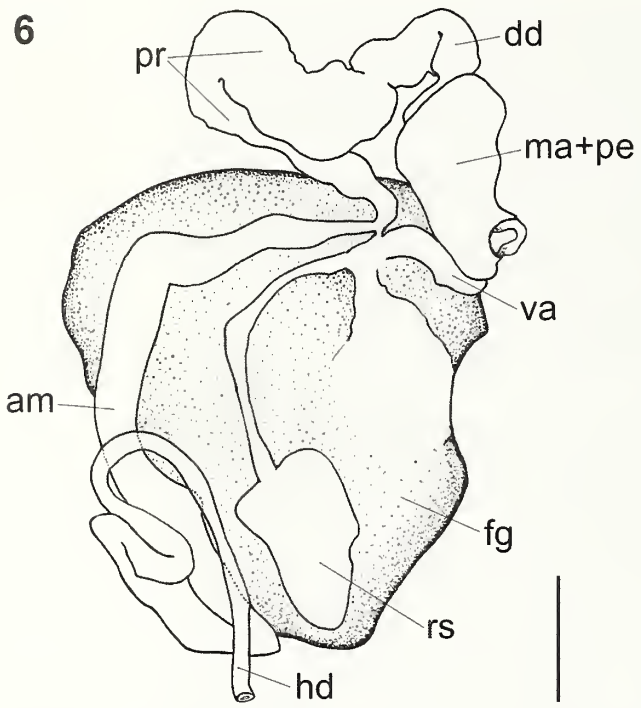


Figure 6. *Cerberilla potiguara* new species, holotype (MNRJ 15111), reproductive system. Scale bar = 1 mm. Abbreviations: **am,** ampulla; **dd,** deferent duct; **fg,** female gland; **hd,** hermaphroditic duct; **ma,** male atrium; **pe,** penis; **pr,** prostate; **rs,** receptaculum seminis; **va,** vagina.

dorsum. Gonopore on right side, below third row of cerata. Anal and renal openings on right side, behind pericardium, under sixth row of cerata. Left side of body of holotype with a cut, made previously, from head to middle region.

Coloration: Body pale yellowish. Some cerata with orange-brown spot located on outer surface, under cnidosac. Cnidosacs whitish and translucent.

Radula and Jaw: Unfortunately, no digestive or reproductive structures were found upon examination of the holotype of *C. tanna*. For description of jaws and radula, see Marcus and Marcus (1960: 259).

Material Examined: Holotype (with the original label). Off Sabine Jetties, Texas, 15 June 1951, 3.6–12 m, Hildebrand col. (MZSP 75244).

Geographic Distribution: Known from Texas, Gulf of Mexico (type locality). The range of this species may include the coast of Mississippi, Florida, St. Vincent and the Grenadines Islands (Ianiello, 2003; Hooper, 2004; Perry, 2005; Wilk, 2005; Valdés et al., 2006).

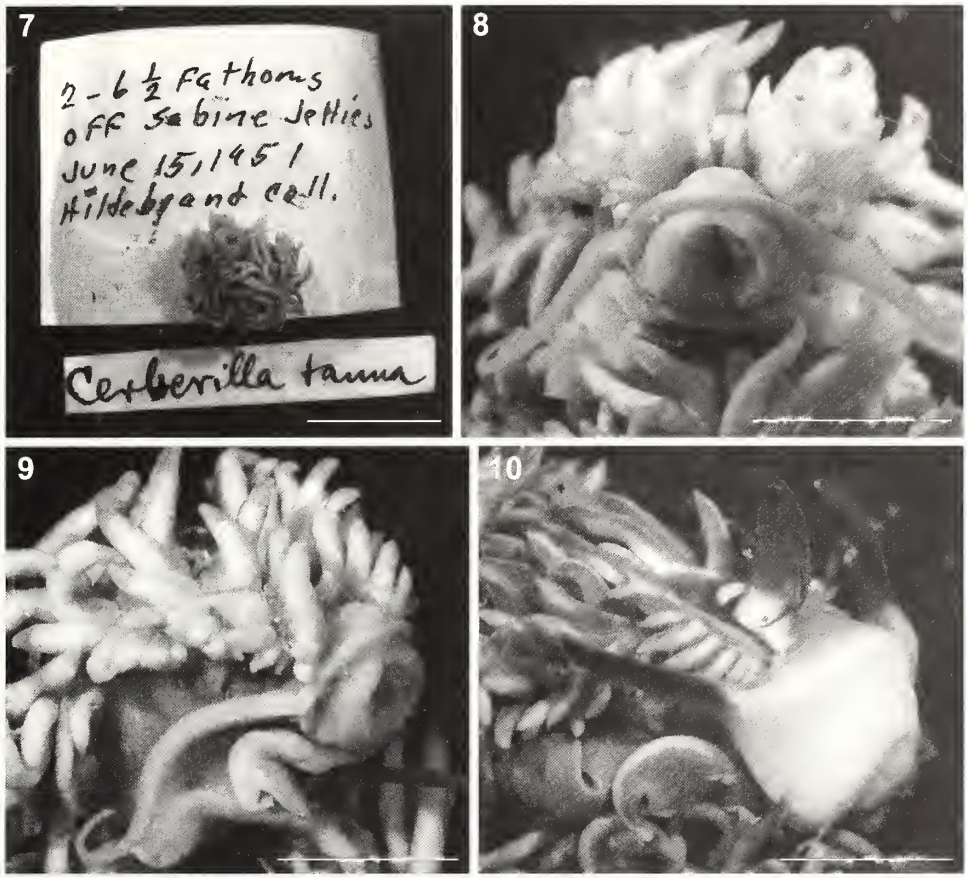
DISCUSSION

Cerberilla potiguara new species is included in the genus by having large, strong and pectinate radular teeth with high marginal denticles; foot wider than the body with distinct tentaculiform anterior corners; small, cylindrical, smooth rhinophores; and penis large and unarmed, according to the definitions given by Bergh (1873), Burn (1966), and McDonald and Nybakken (1975). The last characteristic (penis large and unarmed) was reported originally by Bergh (1873) but was not discussed in subsequent studies.

The characteristics herein observed in the holotype of *Cerberilla tanna* agree with the original description of Marcus and Marcus (1960), including the very short rhinophores, long oral tentacles (around 1/3 of the preserved body length) and the orange-brown spot on the outer face of some cerata. These characteristics contrast with the morphology and coloration of *Cerberilla potiguara* new species, which has longer rhinophores, shorter oral tentacles (around 1/6 of the preserved body length) and a light spot on the outer face of each dark cerata (see Figures 8–10). *Cerberilla potiguara* new species has a longer body with a relatively narrower foot when compared to *C. tanna*, which has an oval foot. Although only one specimen of each species was available for study, remarkable differences could be observed in relation to their internal morphology. The radular teeth of *Cerberilla potiguara* new species have long and short, irregularly arranged denticles, with a sequence of high submarginal and up to three high central denticles. In contrast, the teeth of *C. tanna* have a sequence of alternating short and high denticles, with one to three small denticles between high denticles, and four to seven small denticles of different sizes in the center of the tooth, with the median denticles minute (Marcus and Marcus, 1960, Fig. 19).

Information on the reproductive system morphology is available for few species of *Cerberilla*: *C. affinis* Bergh, 1888; *C. ambonensis* Bergh, 1905; *C. bernadettae* Tardy, 1965; *C. chavezi* Hermosillo and Valdés, 2007; *C. longicirrha* Bergh, 1873; and *C. moebii* (Bergh, 1888). No general characterization about the shape and organization of the reproductive structures exists for the genus. After checking previous descriptions and the morphology of *C. potiguara* new species, some characteristics shared among the species could be observed, including the presence of a large unarmed penis, associated in most cases with a conical atrium; a wide prostate and deferent duct; a small oval receptaculum seminis connected by a narrow tube, which is elongated in most species; and a long, convoluted ampulla. These characteristics are shared by *C. potiguara* new species, *C. affinis*, *C. bernadettae*, *C. chavezi*, and *C. moebii* (see Bergh, 1888, 1888a; Tardy, 1965; Gosliner, 1985; Hermosillo and Valdés, 2007). For *C. ambonensis* and *C. longicirrha*, only references to penis morphology exist, for the former relative to its length (2 mm; Bergh, 1905: 226) and for the latter to the penis length and shape: long and conical (Bergh, 1873: 28). The prominent unarmed penis associated with a conical atrium is herein considered a distinguishing characteristic of the genus *Cerberilla* among the Aeolidiidae.

The elucidation of the identity of the western Atlantic blue morphotype of *Cerberilla*, i.e., corresponding to the



Figures 7–9. *Cerberilla tanna*, preserved holotype (MZSP 75244), external morphology. **7.** Holotype and original labels. Scale bar = 10 mm. **8.** Frontal view of the oral region. Scale bar = 2.5 mm. **9.** Right side view of the anterior portion of the body. Scale bar = 2.5 mm. **10.** *Cerberilla potiguara* new species, preserved holotype (MNRJ 15111), right side view of the anterior portion of the body. Scale bar = 3 mm.

new species herein described, elarifies, at least in part, the situation of the genus in the western Atlantic. *Cerberilla tanna* resembles more the pale-eream morphotype from the Gulf of Mexieo, Mississippi and St. Vincent (Hooper, 2004; Perry, 2005; Wilk, 2005) than the pale-eream morphotype from Florida (Ianiello, 2003; Valdés et al., 2006) beeause the former has short rhinophores and very long oral tentaeles, as originally described and herein observed for the holotype of this speeies. Although it might be a different species, we do not diseard the possibility that the material from Florida represents a juvenile eolor form of *Cerberilla potiguara* new species, as eommented by Rudman (2003) and supported by the existence of other speeimens with less blue pigmentation (Behrens, 2003; Ferretti, 2009; McVicar, 2009). The answers to this and other remaining questions about western Atlantic *Cerberilla* depend on more field observations and anatomieal studies, when speeimens beeome available.

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A new species of *Holospira* (Gastropoda: Pulmonata: Urocoptidae) from Coahuila, Mexico

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ABSTRACT

A new trilamellate *Holospira* Martens, 1860 from southeastern Coahuila, Mexico is described and assigned to *Holospira* sensu stricto. The species is found near the summit of Sierra La Viga at 3,600 meters (11,810 feet), a new elevation record for the genus; however, *Propilsbrya koestneri* Rehder, 1940 is found at a similar elevation.

Additional keywords: Landsnail, lamella, whorl, Sierra La Viga

INTRODUCTION

The urocoptid genus *Holospira* Martens, 1860 is comprised of moderately small species of landsnails bearing cylindroconic to turriform, nondecollate, tightly coiled shells. They have a hollow internal column that usually exhibits a lamella (columellar/axial) within the penultimate whorl. Up to three additional internal lamellae may be present (parietal, basal, and palatal), arising from the upper, lower, and outer walls of the shell respectively. When only three lamellae are present, the combination consists of the columellar, parietal, and basal; the palatal is lacking (see Pilsbry, 1946; Thompson and Mihalcik, 2005). Thompson and Mihalcik (2005) noted that in the sequence of ontogenetic development of the shell, the palatal is the last lamella to form. The species described herein exhibits this trilamellate condition.

Holospira is a prolific and widespread genus typically inhabiting isolated limestone outcrops from the southwestern United States (Arizona, New Mexico, and Texas) to southern Mexico (Oaxaca). The new species is found near the summit of Sierra La Viga in the northern Mexican state of Coahuila at 3,600 meters, the highest known elevation site for a *Holospira*. This mountain is near the northern end of the Sierra Madre Oriental, the major mountain range of eastern Mexico. The previously known elevation record for a *Holospira* was 2,896 meters (9,500 feet; Bartsch, 1906) for *H. nelsoni* Pilsbry, 1903, from the more westerly Sierra Guadalupe, Coahuila. However, another urocoptid species, *Propilsbrya koestneri* Rehder, 1940, from nearby Nuevo Leon, is found at 3,650 meters, slightly higher than *H. fergusoni* new species.

MATERIALS AND METHODS

Shells of the new species were hand-collected by George M. Ferguson on 22 May 1986.

For the scanning electron micrograph of the embryonic whorls, the uncoated holotype shell was mounted on a copper stub with carbon-conductive tabs (PELCO tabs). The micrograph was taken with a Hitachi S-3000N scanning electron microscope.

Abbreviations of institutions used in this article are as follows: CNMO, Colección Nacional de Moluscos (Mexico); LACM, Natural History Museum of Los Angeles County; SBMNH, Santa Barbara Museum of Natural History; UF, Florida Museum of Natural History, University of Florida.

SYSTEMATICS

Superfamily Urocoptoidea Uit de Weerd, 2008
Family Urocoptidae Pilsbry and Vanatta, 1898
Subfamily Holospirinae Pilsbry, 1946
Genus *Holospira* Martens, 1860
Subgenus *Holospira* sensu stricto

Holospira fergusoni new species
(Figure 1, Table 1)

Diagnosis: Shell medium brown, with a moderately attenuate cone gradually enlarging into a stout, cylindric basal region. Armature of three lamellae with greatest development in antepenultimate or first part of penultimate whorl. Peristome slightly expanded on basal and columellar margins, otherwise simple.

Description (Figure 1; Table 1): Shell dextral, cylindroconic, average in size for a *Holospira*, uniformly brown in color, whorls 14.5–15.1 in number. Cone

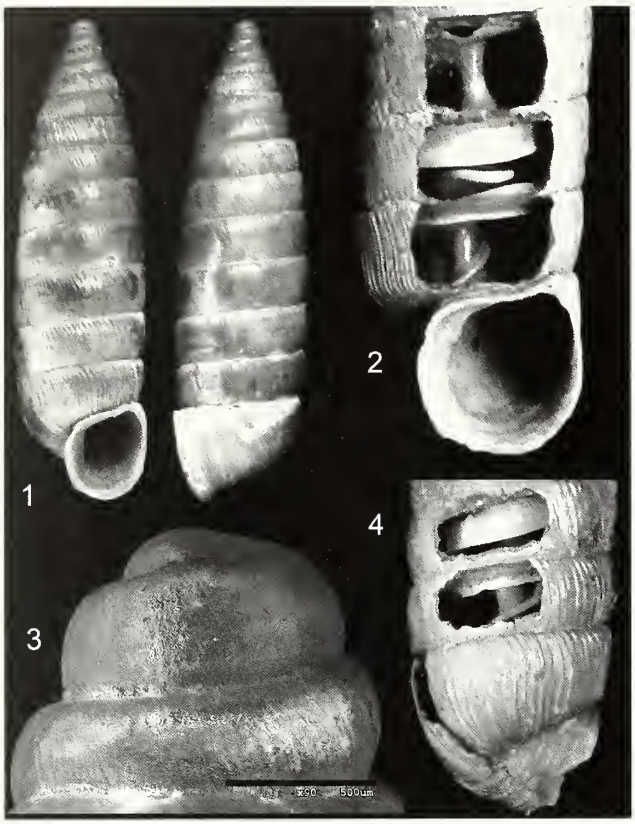

Figure 1. *Holospira fergusoni* new species. **1.** Holotype (LACM 3112), apertural and side views, shell 14.7 × 4.1 mm. **2.** Paratype (CNMO 2562a), shell broken to expose an apertural view of columella and lamellae, maximum shell width 3.9 mm. **3.** Holotype, SEM of embryonic whorls, scale bar = 500 µm. **4.** Paratype (CNMO 2562b), shell broken to expose side view of columella and lamellae, maximum shell width 3.8 mm.

Table 1. Shell measurements (mm.), whorls and number of lamellae of *Holospira fergusoni* new species. Mean measurements include holotype. Paratype at SBMNH broken, not measured. Ap. = aperture; * indicates that apex of shell is broken off, measurement not used for mean.

Shell	Length	Width	# Whorls	Ap. height	Ap. width	Lamellae
Holotype	14.7	4.1	15.1	2.5	2.3	3
Paratypes						
CNMO 2562a	14.0	3.9	14.3	2.4	2.5	3
CNMO 2562b	13.0*	3.8	11.0*	2.0	1.9	3
UF 425856	13.0	3.8	14.5	2.0	2.1	3
$\bar{x}$	13.9	3.9	14.6	2.2	2.2	3

moderately attenuate, gradually enlarging into a stout, cylindric, basal region. Embryonic whorls smooth, 2.6 (holotype) with first 1.6 moderately inflated and steep-sided. Subsequent whorls of cone about 6.5, gradually enlarging, convex; costate, with numerous, well-defined, retractively slanted axial riblets having interspaces about equal in width to riblets. Whorls of cylindric portion of spire about 4.5–5.0, fairly equal in size but widest at antepenultimate whorl, imperceptibly tapering into whorls of cone apically and penultimate and body whorls basally, flattened but with marked suture, very slightly wider at upper margin giving a hint of (upward) overlapping at suture; riblets less pronounced than on cone (usually becoming semi-obsolete between whorls of cone and penultimate whorl), vertical to slightly retracted, thin, numerous (ca. 77 on antepenultimate, 75 on penultimate whorls of holotype), occasionally discontinuous. Body whorl barely extended and slightly descending at peristome, ribbed (or smoothish but becoming ribbed near aperture). Aperture auriculate (extended at upper-outer angle), about as wide as high; peristome slightly expanded along basal and columellar margins, otherwise simple. Umbilicus narrowly perforate.

Internal column, hollow, narrow in apical two-thirds of shell; slowly increasing in diameter as animal grows to adulthood (about 0.15–0.18 times width of shell at penultimate whorl); trilamellate. Greatest development of armature occurs in antepenultimate or first third of penultimate whorl. Columellar lamella large, thick, arising slightly below mid-whorl and extending laterally at least 0.5 times width of lumen in first part of penultimate whorl, becoming sinuous at maximum development, tapering and spiraling basally through first half of body whorl. Parietal lamella a smooth (nonserrated), pendant, wide band, very slightly reflected toward outer wall of shell in last half of antepenultimate and first half of penultimate whorls, sometimes occluding view of columellar lamella (Figure 1, lower right image), becoming reduced in last half of penultimate whorl, then decreased to a low crest in first half of body whorl. Basal lamella a short, low, rounded arch. Palatal lamella lacking.

Type Material: Holotype: LACM 3112; Paratypes: CNMO 2562 a, b (two shells); SBMNH 84922 (one shell); UF 425856 (one shell).

Other Voucher Specimens: CNMO 3168, *Helicina* sp. (one shell); CNMO 3169 *Omphalina* sp. (6 shells).

Type Locality: MEXICO, Coahuila, Municipio Arteaga; Sierra La Viga, 0.5 km E of summit, 25°21′35″ N, 100° 33′15″ W; elevation 3,600 m. The site is approximately 55 km ESE of Saltillo, near the border with the state of Nuevo Leon. Shells of the new species were found under boulders on the North-facing slope of a limestone ridge. In addition, a shell of *Helicina* sp. and several shells of *Omphalina* sp. were found at the site. The area is forested with the dominant plant species being *Pinus hartwegii*. The site is rather difficult to get to.

Etymology: The new species is named after George M. Ferguson of the University of Arizona, Tucson, who collected the shells. A herpetologist by training, his interests also include plants and mollusks. He has always

shared his landsnail collections from remote places with us.

Remarks: The unique internal lamellae of *Holospira* species are typically used as characters for taxonomic purposes. Several subgeneric and section taxa have been based solely on the number and combinations of these lamellae, leading to a confusing array of names and eventual synonymics. Classically, the nominate subgenus (or "section") has been defined by the presence of all four lamellae in the penultimate whorl (Dall, 1895; Pilsbry, 1903, 1946). Additional section names were erected (primarily in the U.S.) for species having 0, 1, or 2 lamellae (Dall, 1895). Bartsch (1906) proposed the subgenus *Tristemma* for trilamellate species (Type species: *Holospira ferrissi* Pilsbry, 1905; Arizona) and later (1945) replaced it (preoccupied name) with *Malinchea*. Pilsbry (1946), noting that no external shell character is correlated with the number of lamellae, and that several U.S. species such as *H. ferrissi* exhibit widely variable numbers (1–3), synonymized *Tristemma*, *Malinchea*, and others with the subgenus *Bostriehoeentrum* Strebel, 1880. A few years later, he (Pilsbry, 1953) stated that "the supposed subgenera based on the number of internal lamellae merely represent parallel stages in evolution." Under the heading of "*Holospira s.str.*," he suggested that four trilamellate Mexican species of *Tristemma* and *Malinehea* described by Bartsch should be "...viewed as species of *Holospira* which have lost that (palatal) lamina, and not relatives of *H. ferrissi* of Arizona..." He proceeded to describe a trilamellate species, *H. maxwelli*, and place it in *Holospira s.s.* (however, leaving *Bostriehoeentrum* unchanged). At the same time, he introduced subgenus *Prionoloplax* for a trilamellate species that exhibits a serrated parietal lamella. Bequaert (Bequaert and Miller, 1973) working in Arizona, synonymized *Tristemma* and *Malinehea* (and others) with a bilamellate subgenus, *Eudistemma* (Dall, 1895). Later, Schileyko (1999) synonymized *Tristemma*, *Malinehea*, *Bostriehoeentrum* and *Eudistemma* (and others) with *Holospira* sensu stricto. Thompson and Mihalcik (2005) assigned several trilamellate species from southern Mexico, to *Holospira* sensu stricto. More recently, Thompson (2008) listed *Eudistemma*, *Tristemma*, and *Malinehea* as synonyms of the nominate subgenus. Based on the foregoing, the trilamellate *H. fergusoni* new species is presently assigned to *Holospira* sensu stricto.

The new species resembles the tetralamellate *Holospira* (*H.*) *amalthea* Bartsch, 1926 from nearby Monterrey, Nuevo Leon. *Holospira amalthea* exhibits a similarly shaped, brown shell that has the greatest development of its lamellae in the antepenultimate whorl. These lamellae are generally comparable to those of *H. fergusoni* new species, except that the parietal is decidedly out-curved at its free margin, the basal is more strongly developed, and the palatal is present (and strong). *Holospira amalthea* also differs by having a broadly expanded and reflected outer lip of the peristome.

Holospira fergusoni new species also shows some similarities to *Holospira* (*H.*) *nelsoni* and *H.* (*H.*) *infanta* Bartsch, 1906 from the Sierra Guadalupe, a range approximately 50 km W of Saltillo. However, *H. nelsoni* is larger, white in color (with blue flecks), and has a more rounded spire than that of the new species. *Holospira infanta* is similar to *H. nelsoni* but much smaller. The shells of both species have all four lamellae contained primarily in the penultimate whorl.

It is noteworthy that the reproductive system of *H. nelsoni* is the only published account of this system from a species assigned to *Holospira* sensu stricto living in this region (Pilsbry, 1903). Although different in certain respects, it shows similarities to that of *H. ferrissi* (type of *Tristemma*) and similar nearby U.S. species (i.e. *Eudistemma* sensu Bequaert and Miller) with regard to the presence of longitudinal internal penial folds (showing through), a long epiphallus, a similar appearing spermatheca, and the presence of a spermathecal diverticulum (see Gilbertson, 1993; Schileyko, 1999). Hopefully, additional descriptions of reproductive systems from species inhabiting this region will be available in the near future.

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Rolleia oberi new species—first record of the genus from the Dominican Republic, with a lectotype designation of *Cyclotus martensi* Maltzan, 1888 (Gastropoda: Annulariidae)

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ABSTRACT

The annulariid genus *Rolleia* Crosse, 1891, previously known only from Haiti, is recorded here from the Dominican Republic: *Rolleia oberi* new species. The syntype lot of a second *Rolleia*, *Cyclotus martensi* Maltzan, 1888 was found to consist of three different species. A lectotype is herein designated.

INTRODUCTION

Bartsch (1946) listed over 200 nominal species of annulariids for Hispaniola; only Cuba contains more taxa of this family. Nevertheless, an examination of Bartsch's localities reveals that there are areas of Hispaniola that had not been adequately studied and that will undoubtedly prove to harbor additional, new taxa. The northern provinces of the Dominican Republic and the western half of the Barahona Peninsula are such areas. Recent collections in these regions have revealed not only new species but range extensions of Haitian genera. This study describes a new Dominican Republic species of the "Haitian" genus *Rolleia*. Abbreviations: BMSM: The Bailey-Matthews Shell Museum, Sanibel, Florida, USA; OSUM: Ohio State University Museum of Biological Diversity, Columbus, Ohio, USA; UF: Florida Museum of Natural History, Gainesville, Florida, USA; ZMB: Museum für Naturkunde Berlin, Germany.

Rolleia Crosse, 1891

Type Species: *Cyclotus martensi* Maltzan, 1888, by original designation

Rolleia oberi new species
(Figures 1–6)

Description: Shell small-sized for family (holotype 8.1 mm maximum length, including peristome × 10.3 mm maximum width, including peristome), thin, fragile, somewhat depressed helicoid, umbilicus very wide (holotype 36 % of maximum width), circular until final whorl, then elliptical, all whorls visible in umbilicus. Protoconch whorls 1.5, not demarcated from teleoconch, smooth, minute but prominent. Teleoconch of 3.0–3.5 whorls, last $1/8^{th}$ turn free from previous whorl and deflected anteriorly. Suture impressed. Peristome double, circular (holotype 3.0 mm diameter maximum inner aperture height × 3.1 mm diameter maximum inner aperture width; holotype 4.3 mm diameter maximum outer peristome height, somewhat broken × 4.6 mm diameter maximum outer peristome width, somewhat broken). Outer lip thin, expanded perpendicular to whorl, narrowest facing umbilicus, touching previous whorl in well-preserved specimens. Inner lip protruded, tube-like, prominent. Inner lip bears same axial sculpture and appears as only a continuation of body whorl beyond juncture of outer lip. Spiral sculpture absent. Axial sculpture of regularly spaced, narrow lamella (ca.100 on final whorl), interstices smooth. Suture broken by axial lamella. Teleoconch dirty-white or crystalline, most specimens without any apparent pattern although some show faint tan rays on outer lip. Nuclear whorls may have a brown peripheral band. Operculum thin, multispiral with wide lamellum, originating perpendicularly to basal plate, then curling outward to parallel basal plate. Anatomy and radula unknown.

Type Material: Holotype: UF 434775, Dominican Republic, Puerto Plata Province, La Has, El Puerto, on the road about half way between Santiago and Puerto Plata, at altitude 830–1000 m in the Cordillera Septentrional; Paratypes: UF 434776 (9.7 mm maximum length, including peristome × 9.2 mm maximum width, including peristome), UF 434776, (6.1 × 5.0 mm, juvenile), UF 434776, (6.0 mm × 5.0 mm, juvenile), BMSM 17970 (6.7 × 8.2 mm), BMSM 17970 (7.3 mm × 10.0 mm), OSUM 35489 (2 specimens, 7.4 × 9.2, 7.9 × 10.1 mm), all from the type locality.

Other Material Examined: Watters collection, GTW 14180a, 2 specimens (1 juvenile), from type locality.

Figures 1–6. *Rolleia oberi* new species, all from the Dominican Republic, Puerto Plata Province, La Has, El Puerto, on the road about half way between Santiago and Puerto Plata, at altitude 830–1000 m in the Cordillera Septentrional. **1–4.** Holotype UF 434775, 10.3 mm maximum width. **5.** Paratype UF 434776, 9.2 mm maximum width. **6.** Paratype OSUM 35489, 9.2 mm maximum width. **7–9.** Holotype USNM 504088 of *Rolleia haitensis* Bartsch, 1946, from Ennery, Haiti, 15.1 mm maximum width. **10, 11.** Lectotype ZMB 40725a of *Cyclotus martensi* Maltzan, 1888, from Plaisance, Haiti, ca. 15 mm maximum width. Courtesy Malacological Collection, Museum für Naturkunde Berlin, Leibniz Institute for Research in Evolution and Biodiversity at the Humboldt University [photography L. Maitas].

Comparison with Similar Species: *Rolleia oberi* differs from both *Rolleia haitensis* Bartsch, 1946 and *Rolleia martensi* (Maltzan, 1888) in having a higher spire, axial sculpture developed into sharp lamellae rather than low threads, and in the more laterally produced outer lip.

Distribution: Known only from the type locality. *Rolleia* was previously known only from two species, *R. haitensis* and *R. martensi*, both from the Ennery-Plaisance region of the Massif du Nord of Haiti. *Rolleia oberi* occurs ca. 200 km to the east in the Cordillera Septentrional of the Dominican Republic; this is the first record of the genus from that country.

Discussion: Maltzan (1888) described *Cyclotus martensi* from "Plaisance in parte boreali insulae Haiti" without illustration. Bartsch (1946: 141), in his discussion of that species, makes no mention of having seen the type material but based his description of it on USNM specimens "collected by Orcutt on limestone rocks 40 miles south of Cap-Haïtien." Bartsch may have based his identification on the illustration of Crosse (1891: pl. 2, fig. 4) although there is no evidence that Crosse had seen the type lot either. (Wenz's [1939: fig. 1471] illustration of *C. martensi* is too crude to be positively identified). Bartsch then described *Rolleia haitensis* (Figures 7–9) from Ennery, with additional localities of "on the mountain summit between Ennery and San Michel," "14 miles north of Gonaïves," "15 miles north of Gonaïves," and "on Peterborough Mountain" (1946: 142). All of these sites are within a fairly close distance of each other in the Massif du Nord.

The syntype lot of *Cyclotus martensi* at ZMB consists of six specimens that were the combination of Maltzan's lots 40725 and 41177 (now both 40725). Lot 40725 is from Plaisance-Gonaïves, lot 41177 is from Plaisance. Which of the six specimens originally went with which lot is not known. This combined lot contains all three species of *Rolleia*, including the new species described here: four specimens of *C. martensi* and one specimen each of *Rolleia haitensis* and *Rolleia oberi*. With the exception of shell size, Maltzan's original description has little to identify which of the six specimens was used to describe *C. martensi*. But he gave the "Diam. maj." as 14–16 [mm], apparently including more than one specimen. This eliminates his specimen of *R. haitensis*, which is only 11 mm in maximum diameter, as well as his specimen of *R. oberi*, which is only 10 mm. The remaining specimens are indeed all between 14 and 16 mm in maximum diameter and therefore are the only specimens in the type lot that could respresent *C. martensi*. To avoid future confusion we designate ZMB 40724a as the lectotype (Figures 10, 11) of *Cyclotus martensi* and the remaining three specimens (ZMB 40725b) as paralectotypes. In addition we remove the specimens of *R. haitensis* and *R. oberi* from the type series of *Cyclotus martensi*.

What remains to be explained is how a specimen of *R. oberi* (and *R. haitensis*) ended up in the type lot of *C. martensi*. Maltzan's only paper on annulariids described species from Haiti collected by the German shell dealer Hermann Rolle in 1887–88. *Rolleia oberi* is not known from the Massif du Nord where *R. haitensis* or *R. martensi* are recorded, nor from Haiti in general. Unless *R. oberi* occupies a much larger area than described here, which is unlikely, it must be the case that additional lots were somehow mixed.

Etymology: Named for Jim Ober, who assisted GD in the collection of the specimens.

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Las Conchas Azules (The Blue Shells): Father Kino, abalones, and the Island of California

Dedicated to Helen DuShane (1907–2002)

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The First International Conference on the Zoogeography of Northeast Pacific Abalones was convened by the Italian Jesuit, Father Eusebio Francisco Kino, 30 April–1 May 1700. It was held at Bac (≈32° 06′ 20″ N; 111° 00′ 30″ W), the largest Sobaipuri village on the Río Santa Cruz, in the Spanish Gobernación of Nueva Vizcaya. Also in attendance were members of the Pima (= O'odham), Opata, and Cocomaricopa nations, discussing the origin of abalone shells obtained in trade from the Yuma and Cutgane peoples of the Colorado River. These beautiful items were called the blue shells (*las conchas azules*).

Studies of molluscan biogeography are dependent upon good mapping and correct identification of localities. Numerous cases in the literature report erroneous type localities, and misnamed or improperly described collecting areas. Tenacious beliefs in a mythical place can replace or suppress topographic evidence. This paper describes a curious instance of how proper documentation of the distribution of a mollusk changed the maps of an area.

"I hold it to be very certain and proven that the whole kingdom of California, discovered on this voyage, is the largest island known or which has been discovered up to the present time" (Father Antonio de la Ascención, from his journal written during Vizcaino's 1602 voyage along the coasts of the modern three Californias, from Cabo San Lucas to Monterey, although they never found its northern terminus). Earlier, Juan Rodríguez Cabrillo had made the first voyage along the Pacific coast (1542–1543), reaching Cape Mendocino, seeing land during the entire journey. But the mythical Calafia would not disappear. Despite Francisco de Ulloa's (1539) sailing the Sea of Cortez entirely to its northern end, and Juan de Oñate's 1604–05 descent of the Colorado River to a view of the Sea of Cortez, in the 1500 and 1600s the commonly held (and mapped) European belief was in the insular status of California.

Thirty years of explorations, missionary activities and mapping throughout Lower California and the Pimería Alta by Father Eusebio Kino, S.J., dealt the final and complete blow to the "island of California."

Father Kino's two missionary efforts in California at La Paz (Spring–Summer 1683) and San Bruno (October 1683–May 1685) were religious failures. However, during his 20 months at Misión San Bruno (north of present-day Loreto), he made several expeditions westward trying to cross the steep and forbidding barrier of the Sierra de la Gigante. Having gotten directions from the regional Cochimí inhabitants, he traversed passes, arroyos and stream beds that finally led him to the shores of the Pacific Ocean on 30 December 1684, his third attempt. The explorers named the site Bahía Año Nuevo, but today it is known as San Gregorio (approximately 26°03′ N; 112°17′ W). Meandering along the beach, he chanced upon some large, beautiful blue shells.

Returning to mainland Mexico, he was assigned to missionary work in the Alta Pimería (north-central Sonora and southwest Arizona). While laboring among the various Pima peoples for years, he harbored a zealous concern for the establishment and provisioning of missions in Lower California.

During 21–23 February 1699, while preaching to the Pimas and Yumas at San Pedro (near the junction of the Gila and Colorado Rivers), Kino first saw the blue abalone shells on the mainland, which he had originally seen 14 years earlier on the Pacific coast of Lower California. He wrote in his journal, "These natives of San Pedro in the two days when we were with them gave us various beautiful blue shells, which, so far as I know, are found only on the opposite or western coast of California. Afterward it occurred to me that not very far distant there must be a passage by land to near-by California" (Bolton, 1919: 195–196; hereafter cited as MPA) which would provide a possible land route to provision the missions of Lower California.

He had previously made expeditions to the northern Gulf, and had seen "plainly that that arm of the sea kept

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getting narrower," and even "descried most plainly both with a telescope and without a telescope the junction of these lands of New Spain with those of California, the head of this Sea of California." When the natives gave him the blue shells, "still it did not occur to me that those blue shells must be from the opposite coast of California and the South Sea, and that by the route by which they had come thence, from there to here, we could pass from here thither, and to California" (MPA: 229–230).

A few months later, Kino took 10 Pimas and 53 mules and horses north from his home mission at Dolores to found Misión San Xavier del Bac (near present-day Tucson). He dispatched various messengers throughout the surrounding nations of indigenous people, "to learn with all possible exactness in regard to the blue shells and the passage by land to California" (MPA: 234–235).

The participants at this First International Conference on the Zoogeography of Northeast Pacific Abalones all asserted that these blue shells "came from the opposite coast of California and from the sea which is ten or twelve days' journey farther than this other Sea of California, on which there are shells of pearl and white, and many others, but none of those blue ones" (MPA: 237–238).

After several more expeditions to the Gulf of California, he had assembled his evidence of the "peninsularity" of Lower California: presence on the mainland of the blue shells from the west coast of the peninsula, sightings from the junction of the Gila/Colorado Rivers showing no intervening body of water to separate the two regions, and statements of the indigenous people living near the head of the Gulf.

In late 1701, he redrew his earlier 1695 "insular" map (Figure 1). After it was printed in 1705 (Figure 2), it became one of the best known maps of northern New Spain. That Lower California was a peninsula was never again in doubt.

Joshua L. Baily, Jr. (1935), wrote that "the first collection of west coast shells was the work of Father Eusebio Francisco Kino," predating the conchological efforts of Cook and Martyn (in 1784), Dixon (1789) and Eschscholtz (1822), which had been cited by Philip P. Carpenter as the first collectors. Baily based his comments on Eldridge (1915), apparently unaware of Bolton's publication of MPA. Although writing that "We do not even know what the shells were, for his description—'beautiful blue shells'—is too meager to be considered anything but a *nomen nudum*," he tried to "make a pretty good guess" (Baily, 1935: 75). Baily identified the species as *Olivella biplicata* (Sowerby, 1825) for three reasons:

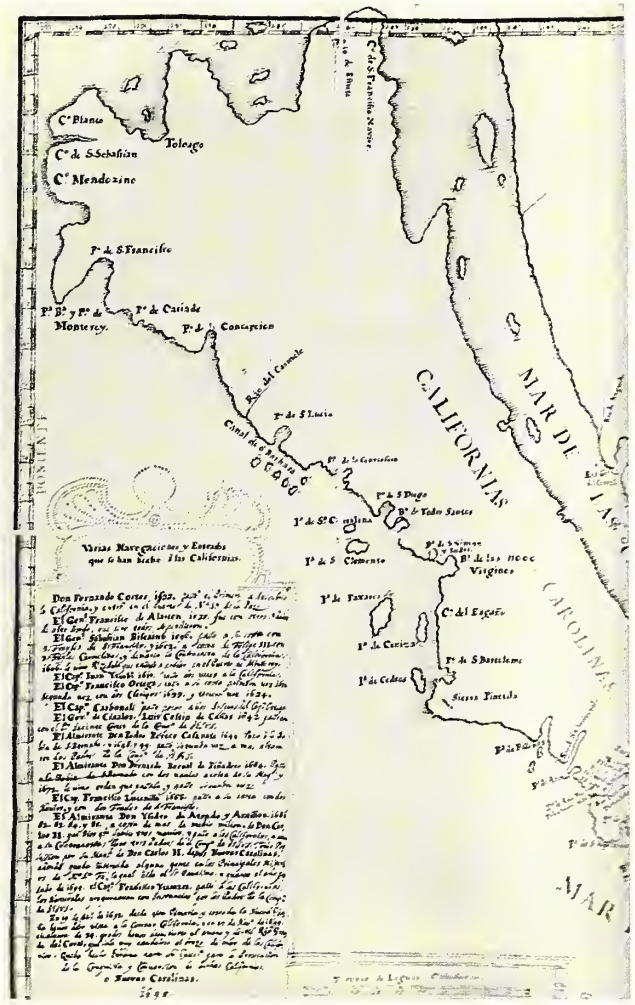

Figure 1. Father Eusebio Francisco Kino's 1695 map, showing Lower California as an island (from Burrus, 1965).

Figure 2. Father Kino's 1701 map (first published in 1705) showing Lower California as a peninsula (from Burrus, 1965).

- It is "the most popular shell for wampum purposes among the Indians of Arizona today";
- "The lower part of the columella is almost universally azure tinted"; and
- Its geographic distribution (ranging southward along the California Pacific coast to Bahía Magdalena; absent from the Gulf).

However, statues of Kino in Hermosillo, Sonora, Mexico, and in his hometown of Segna, Italy, depict him on horseback, holding an abalone shell (illustrated in Polzer, 1998: 192–194). The plaza mural near his gravesite at Magdalena de Kino (Figure 3) shows him with an abalone shell in his hand. I concur with historians, artists, civic leaders and others that the "beautiful blue shells" were abalone:

- There are several species of *Olivella* occurring in the Gulf of California, which have distinct purple apertural coloring, e.g., *Olivella dama* (Wood, 1828) = *Oliva purpurata* Swainson, 1831). In the 16th century, relying on a 14-year-old memory, an untrained amateur shell collector such as Kino could not have distinguished between different species of *Olivella* with similar whitish or light gray outer coloration, and purple on the inside.
- Size matters. Abalones are impressive, large shells, much bigger than the 20–27 mm long *Olivella biplicata.* Kino had sent Father Marcos Antonio Kappus (Rector of the College of Matape) several of his "blue shells," for which Kappus wrote him, "I esteem the blue shells, and especially the large one, which is a truly rare piece" (MPA: 259–260). The description in Kino's (MPA) and Manje's (Burrus, 1971) journals of these expeditions clearly emphasize both their uniqueness (which would not be the case among similarly colored *Olivella* congeners) and size.
- Eighteenth Century Accounts. While serving in Baja California from 1737–1768, Miguel del Barco investigated the plants, animals and minerals of the peninsula. He wrote about the blue shells: "On the exterior coast there are found some shells, proper to it, which are perhaps the most beautiful in the world. This is because their luster usually is greater and finer than that of the finest mother-of-pearl. These shells are darkened and covered with a pleasant and extremely vivid blue. . . These shells are somewhat deeper than

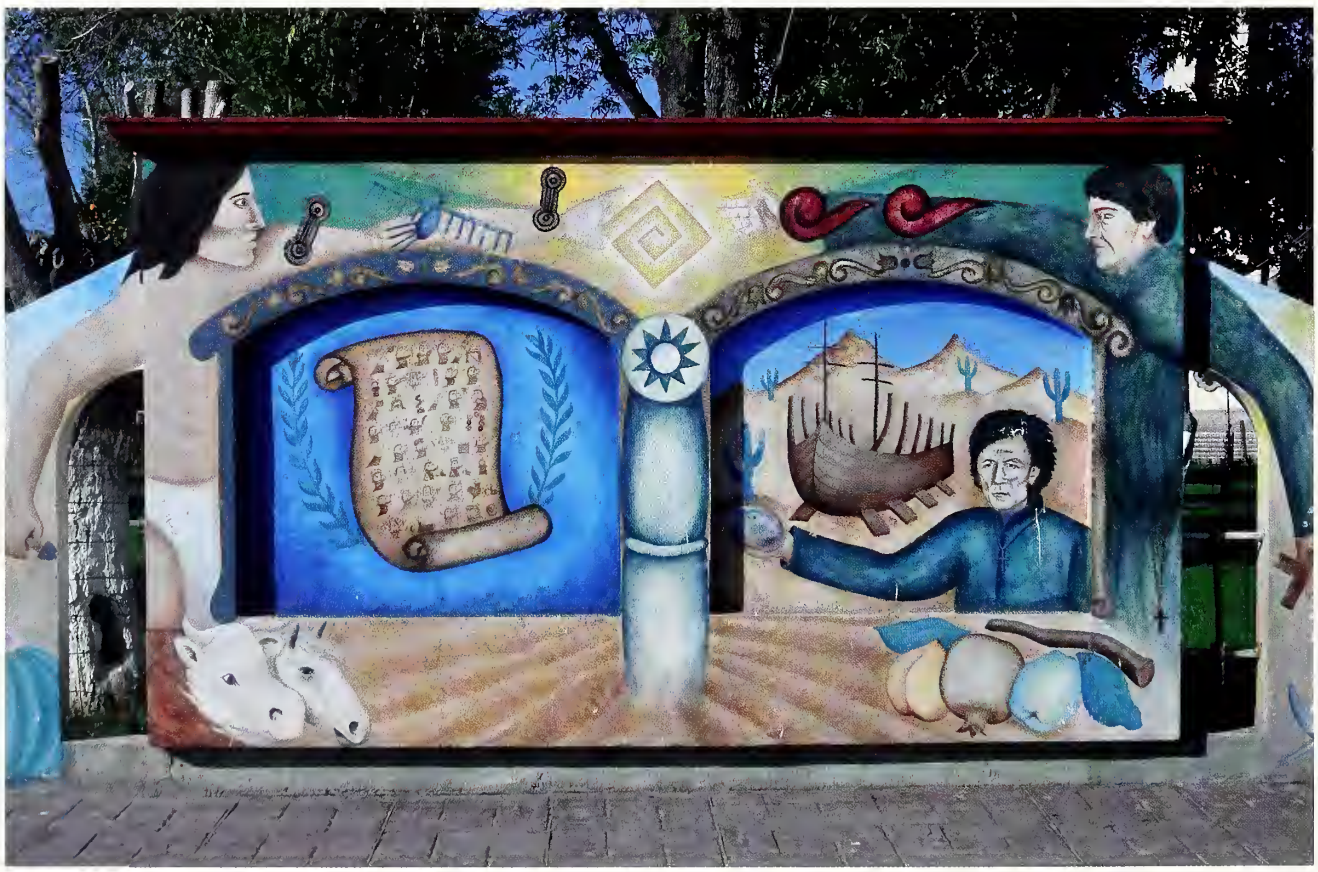

Figure 3. Mural of Father Kino, holding an abalone shell, with depictions of cattle and crops that represent farming skills he introduced to the Pima nations, and tongues of flame symbolic of his linguistic skills and missionary endeavors. Monument at the Main Plaza in Magdalena de Kino, Sonora, Mexico.

ordinary, and on one side only they have five or six round holes" (Barco, 1980: 249–250).

- Ignacio Tirsch, missionary in Lower California from 1762–1768, made the only eyewitness drawings of the plants and animals of the peninsula in Jesuit times. His drawings of California sea shells (Tirsch, 1972) clearly illustrate an abalone, labeled "*concha azul*."
- Historians have considered these magnificent shells to be abalone (e.g., Burrus, 1971: 114; Note 5, Barco, 1980: 249; and Polzer, 1998: 66–70).
- The most likely species-level identification of the specimens is *Haliotis fulgens* Philippi, 1845, which is characterized by an "interior highly iridescent, chiefly blue with overtones of pink and green" (McLean, 1978).

Abalones are distinct, and are obviously present on the Pacific Californian coastline, and similarly absent in the Gulf of California. Father Kino's training as a cartographer, mathematician, and scientist served him well. His studies on Comet Kirch (Kino, 1681), although unabashedly Aristotelian in its views, were one of the earliest scientific works published by an European in the Americas. Because of his astute observations and reasoned questioning, abalones, the geography of California, and a Jesuit priest are inextricably interwoven.

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Research Note

The date of publication of section 16, *corrigenda quaedam et addenda*, of Dunker's *Novitates Conchologicae*, Series II, *Marina Mollusca*

Although the date 1870 was printed on the title page of the final section of Dunker's *Novitates Conchologicae*, Series II, *Marina Mollusca*, (section 16, *corrigenda quaedam et addenda*), that section was erroneously dated 1878 in Johnson's (1969) collation of the work. Johnson's date was based on dated wrappers and other evidence from copies in the library of the Museum of Comparative Zoology at Harvard University and in Johnson's personal library. Pages 137–144 of the *Novitates* were received at the Harvard Library on February 14, 1879, and Johnson's 1878 date is based upon this date of receipt. Prior to Johnson's published collation, this section was dated variously as 1871 and 1876. The date of publication is significant because Dunker described a new species, *Fasciolaria heynemanni*, in the *addenda*, and this information fixes its date of description.

The name *heynemanni* was immediately used and has been well known since its publication, but no one associated a date with the name during its first 100 years except von Martens (1904: 30), who used 1871. After that citation no others were made (with a date) until Kilburn (1974: 206) reiterated the 1871 date. Since that time at least 11 authors have variously used the dates 1871 and 1876.

The 1876 date traces to Kobelt *in* Küster and Kobelt (1876: 139), who cited Dunker's publication and quoted Dunker's description; Snyder (2003) cited that usage as "Dunker *in* Küster and Kobelt, 1876," *i.e.*, a citation of Dunker's work prior to its later publication, but Abbott and Dance (1982: 183), Goto and Poppe (1996: 388), and Mallard and Robin (2005: 8) simply used "Dunker, 1876." As a further complication, Kobelt (1875: 363) also cited the name and a figure in his catalogue, evidently anticipating that his larger (1876) work would be published prior to the catalogue. Ruhoff (1980) is unclear on this issue. Although she cited dates of 1858–1870 for Dunker's *Novitates Conchologicae*, she did not include *Fasciolaria heynemanni* among new names introduced between 1850 and 1870.

We discovered a reference to *Fasciolaria heynemanni* by Tryon (1871: 36) that prompted us to examine the copy of Dunker's work in the library of the Academy of Natural Sciences of Philadelphia. That copy bears a donation label indicating that it was a gift of T.B. Wilson. All gifts to the Academy library are catalogued with the date of the gift, so it was straightforward to find that Wilson made his presentation to the Academy in 1871. Tryon's note was published on 1 August 1871, so Wilson's gift must have been received earlier that year. Article 21.2 of the International Code of Zoological Nomenclature, Fourth Edition (1999) states: "The date of publication specified in a work is to be adopted as correct in the absence of evidence to the contrary." Taking into account the time for sea travel from Germany to Philadelphia, we believe that this section could have been published in 1870, as indicated on its title page. As no clear evidence has been found to indicate an 1871 publication date, we advocate adoption of the 1870 date as specified by the Code.

In other taxonomic actions in this section, Dunker (1871) reclassified *Anomalocardia latruncularia* Römer in the genus *Crytogramma*; placed *Mactra lühdorfi* Dunker in synonomy with *Mactra sachalinensis* Schrenk; and reclassified *Ricinula speciosa* Dunker as a variety of *Ricinula reeveana* Crosse.

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THE NAUTILUS publishes articles on all aspects of the biology, paleontology, and systematics of mollusks. Manuscripts describing original, unpublished research and review articles will be considered. Brief articles, not exceeding 1000 words, will be published as notes and do not require an abstract. Notices of interest to the malacological community will appear in a notices section.

Manuscripts: Each original manuscript and accompanying illustrations should be submitted to the editor preferably via e-mail or as hardcopy in triplicate.

Text must conform to the dimensions of 8½ × 11-inch paper, double-spaced, and single-column throughout (including literature cited, tables, and figure captions). Authors should follow the general recommendations of *Scientific Style and Format—The CSE Manual for Authors, Editors, and Publishers*, available from the Council of Science Editors at www.councilscienceeditors.org. The first mention of a scientific name in the text should be accompanied by the taxonomic authority, including year. Latinized names and other words to be printed in italics must be underlined; leave other formatting indications to the editor. Metric, not English, units are to be used. Geochronologic modifiers should be capitalized only when units are formally recognized: for instance, use Late Cretaceous but early Miocene. Likewise, only modifiers of formally recognized chronostratigraphic units are capitalized: use Lower Jurassic but upper Oligocene.

The sequence of sections should be title page, abstract, introduction, materials and methods, results, discussion, acknowledgments, literature cited, tables, figure captions, figures. The title page should include the title, author's name(s) and address(es). If corresponding author is not the senior author, please indicate. The abstract should summarize in 250 words or less the scope, main results, and conclusions of the article. Abstracts should be followed by a list of additional key words. All references cited in the text must appear in the Literature Cited section and vice-versa. Please follow a recent issue of THE NAUTILUS for bibliographic style, noting that journal titles must be unabbreviated. Information on plates and figures should be cited only if not included within the pagination of cited work. Tables must be numbered and each placed on a separate page. If in doubt, please follow a recent issue of the journal for sequence of sections and other style requirements.

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A new species of *Iothia* (Gastropoda: Lepetidae) from Chilean methane seeps, with comments on the accompanying gastropod fauna

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ABSTRACT

A new species of the limpet genus *Iothia*, *I. megalodon* new species, is described from a cold-seep locality in central Chile. It differs from other species of *Iothia* by the enlarged functional radular teeth. *Iothia megalodon* feeds on bacterial film and sediment as indicated by the gut content. *Iothia emarginuloides* (Philippi, 1868) is re-instated as the name to be used for the Antarctic–South American species previously known as *Iothia coppingeri* (E.A. Smith, 1881). A COI analysis of eight species of Lepetidae is included to elucidate the generic position of the new species. The gastropod fauna of the type locality, the recently discovered bathyal methane seeps off Central Chile, is reviewed in order to place *Iothia megalodon* in its ecological context. *Margarites huloti* Vilvens, 2006, *Bathybembix macdonaldi* (Dall, 1891), *Calliotropis ceciliae* Vilvens and Sellanes, 2010, and *Cantrainea panamense* (Dall, 1908) are known to have relatives in seeps or other chemosynthetic environments. The presence of *I. megalodon* within this community and its gut content support its inclusion as a member of the seep fauna.

Additional keywords: Molecular phylogeny, Chile

INTRODUCTION

The interest in chemosynthetic environments, hydrothermal vents, and various types of seeps has remained at a high level, ever since the discovery of vents in 1977 (Ballard, 1977; Lonsdale, 1977; Corliss et al., 1979). A few years later, the first sulphide seep locality off Florida (Paull, 1984) and methane seeps in the Gulf of Mexico (Brooks, Kennicut and Fay 1985) were discovered. In less than 30 years, these environments have become fairly well known, much better known than the surrounding deep-sea. The Gastropoda is richly represented in seeps and vents, both in number of species and specimens (Warén et al., 2006).

The fauna of vents and seeps to a high extent consists of species that have been found only in these environments (van Dover, 2000), more so in the vents. But there are also species that live in the adjacent deep-sea and seem to be attracted by the higher biomass and more complicated biotope, often with rocks, shells, and soft sediments mixed. To understand the ecology of these biotopes, it is therefore important to know which ones are its regular inhabitants and which are occasional intruders. Recognition of chemosynthetic biotopes is facilitated if this can be done simply from the presence of certain common genera or species when less sophisticated methods of investigation are used, which is the present case.

Already some time ago, species like *Calyptogena australis* Stuardo and Valdovinos, 1988 (Bivalvia, caught by long-line fishery), *Bathybembix macdonaldi* (Dall, 1891), and *Cantrainea panamense* (Dall, 1908) (Gastropoda, from side catches during trawling), started to become available on the commercial shell market. Their presence indicated that seep bottoms could occur off the Chilean coast. This was then confirmed by seismic surveys and trawling off Concépcion in depths between 650 and 930 m (Sellanes et al., 2004, 2008). So far, these seeps have been explored only by trawling and tube-coring.

In this paper, we describe a new patellogastropod from the methane seeps. The terminology largely follows Lindberg's (1998) review of the Patellogastropoda (=Docoglossa). To broaden our base for the systematic placement of the new species, we add some preliminary results from ongoing work on the phylogeny of the patellogastropods in hot vents and cold seeps (Nakano and Warén, unpublished).

To place *Iothia megalodon* in its ecological context, we summarize the gastropod fauna known from the Concépcion seeps, the type locality of *I. megalodon*, since the species have been described in several not easily accessible small papers. We review existing and new information on these species in order to single out which species may be considered "seep fauna".

MATERIALS AND METHODS

Chilean Sampling Sites

The seep specimens originate from several hauls with an Agassiz trawl with an opening of 1.5 × 0.4 m from R/V Vidal Gormáz, off Concepción, central Chile. When the trawl came up, sediment samples were washed on board, specimens were picked out and preserved in 70% ethanol.

Cruise VG-03, 36°21.38′ S, 74°43.91′ W, 980 m depth, Nov. 2003 (*Iothia megalodon*, 2 paratypes, SMNH type collection 6784 and MNHC 6619)

Cruise VG-04, AGT 06, 36°21.75′ S, 73°43.55′ S, 800 m, Oct. 11, 2004. (*Cantrainea panamense* – 3 specimens, SMNH 103188)

Cruise VG-04, AGT 13, 36°21.91′ S, 73°43.21′ S, 843–728 m, Oct. 20, 2004 (*Bathybembix macdonaldi* – 2 specimens - SMNH 103189)

Cruise VG-06, AGT 6, 36°21.67′ S, 73°43.52′ W, 865 m, Sep. 01, 2006. (*Zetela alphonsi* – 2 specimens SMNH 103187)

Cruise VG-06 AGT 7-2, 36°32.19′ S, 73°40.65′ W, 764–843 m, Sep. 03, 2006 (*Iothia megalodon*, 2 paratypes SMNH type collection 7932)

Cruise VG-07, AGT 10, 36°22.01′ S, 73°43.10′ W, 764–843 m, Oct. 02, 2007, (*Iothia emarginuloides* – 1 specimen, SMNH 103936; *Iothia megalodon*, **holotype 6617**, 1 paratype MNHC 6618, 2 paratypes SMNH type collection 7933)

Cruise VG-07, AGT 11, 36°21.88′ S, 73°42.99′ W, 824–730 m, Oct. 03, 2007 (*Margarites huloti* Vilvens, 2006 – 3 specimens SMNH 103190, 103192 [dry]).

Work in the area has indicated several active methane seep sites with assumed chemoautotrophic communities, with chemosymbiotic clams like *Calyptogena, Lucinoma,* and *Thyasira* (Sellanes et al., 2004; Holmes, Oliver and Sellanes, 2005; Oliver and Sellanes, 2005; Sellanes and Krylova, 2005; Sellanes, Quiroga, and Neira, 2008). In addition, the heterotrophic fauna has high population densities within this area, probably benefiting from the abundance of food and by the habitat heterogeneity generated by the carbonate reefs associated with methane seepage (Sellanes et al., 2008).

Morphology

For the systematic work, specimens of *Iothia*, *Margarites huloti, Cantrainea panamense,* and *Zetela alphonsi* were cleaned, soft parts extracted and critical point dried, and the gross anatomy examined with SEM. Radulae were prepared by dissection and cleaning in 1:50 commercial bleach (*Iothia megalodon*), or by dissolving bodies in 25% KOH at 40°C, cleaned, mounted, and examined with SEM.

For comparison with the new species of *Iothia*, DNA was extracted from pieces of foot tissue of the species listed in Table 1 where collection data and localities are listed. In total, 10 individuals were newly sequenced, and combined with published sequences of 9 individuals from Nakano and Ozawa (2007). Two species of *Emarginula* (Fissurellidae) and three species of the Cocculinidae were used as outgroup taxa.

DNA Methods and Phylogenetic Analysis

The procedures described by Nakano and Ozawa (2007) and Nakano et al. (2009) were used to extract DNA, amplify it using PCR, and determine the sequence of the COI and Histone H3 genes. All new sequences determined in this study have been deposited in GenBank (accession numbers in Table 1).

COI and Histone3 sequences were manually aligned using MacClade 4.03 (Maddison and Maddison, 2002), with reference to the translated amino acid sequence. Third-codon positions of both genes were retained in all phylogenetic analyses. The model of nucleotide substitution for the Bayesian analyses were selected using Modeltest (Posada and Crandall 1998), giving GTR+I+G for COI and Histone3. The partition-homogeneity test (Swofford 2002; the ILD test Farris et al. 1995) was performed to test whether the COI and Histone H3 sequences contained similar phylogenetic signal and could thus be analysed as a single data-set. Subsequent phylogenetic analyses were performed with PAUP* version 4b10 (Swofford 2002) for neighbor-joining (NJ) (Saito and Nei, 1987) (Kimura's two-parameter method; Kimura, 1980), equally weighted maximum parsimony (MP), as well as their associated bootstrap values (Felsenstein, 1985, 1988). MrBayes v.3.1.2 (Huelsenbeck and Ronquist, 2001; Ronquist and Huelsenbeck, 2003) was used to perform Bayesian analyses and to estimate posterior probabilities.

The NJ bootstrap analyses consisted of 10,000 replicates. The MP bootstrap analysis consisted of 1,000 replicates using heuristic search (with 10 random addition sequence replicates and TBR branch-swapping).

MrBayes was run with the following settings for the two partitions (i.e., genes), the maximum-likelihood model employed six substitution types (nst=6), rate variation across sites was modeled using a gamma distribution, with a proportion of the sites being invariant (rate=invgamma), the shape, proportion of invariable sites, state frequency, and substitution rate parameters were estimated for each partition separately. The Markov-chain Monte-Carlo search was run with four chains 3,000,000 generations, with trees being sampled every 100 generations and the first 5,000 trees (i.e., 500,000 generations) were discarded as burn-in.

Table 1. Specimens of Lepetidae sequenced for this study.

Species	Locality	Museum Registration	COI	Histone H3
Order PATELLOGASTROPODA				
LEPETIDAE				
Bathylepeta linseae Schwabe, 2006	Antarctica, 70°04.5′S, 03° 20′W, 2084–2163 m depth	ZSM Mol 20081168	AB543973	AB543983
Cryptobranchia kuragiensis (Yokoyama, 1920)	Aicappu, Akkeshi-cho, Hokkaido, Japan, 5–8 m depth.	NUGB-L505	AB238457	AB543984
Cryptobranchia kuragiensis (Yokoyama, 1920)	Aicappu, Akkeshi-cho, Hokkaido, Japan, 5–8 m depth.	NSMT-Mo76949	AB543974	AB543985
Iothia fulva (O.F. Müller, 1776)	Raunefjord, Norway, 50 m depth.	SMNH 107221	AB548309	AB548310
Iothia emarginuloides (Philippi, 1868)	Argentine, Beagle Channel, Bahia Lapataia, 54° 51′S, 068° 33′W, 15–18m depth	SMNH-103867	AB543975	AB543986
Iothia megalodon n. sp.	Chile, methane seep off Concepcion, AGT 10, 36° 22.01′S, 73° 43.10′W, 764–843 m depth.	UG07-AGT10	AB543976	AB543987
Lepeta caeca (O.F. Müller, 1776)	Koster Area, Bohuslän, Sweden	SMNH-65221	AB543977	AB543988
Lepeta caeca pacifica Moskalev, 1977	Aicappu, Akkeshi-cho, Hokkaido, Japan, 2–3 m depth	NUGB-L503	AB238458	AB543989
Lepeta caeca pacifica Moskalev, 1977	Aicappu, Akkeshi-cho, Hokkaido, Japan, 2–3 m depth.	NSMT-Mo76950	AB543978	AB543990
Limalepeta lima Dall, 1918	Urakawa-cho, Hokkaido, Japan, 150–300 m depth.	NSMT-Mo76951	AB543979	AB543991
Limalepeta lima Dall, 1918	Urakawa-cho, Hokkaido, Japan, 150–300 m depth.	NSMT-Mo76952	AB543980	AB543992
Sagamilepeta sagamiensis (Kuroda and Habe, 1971)	Off Hota, Chiba Pref., Japan, 200–270m depth.	NSMT-Mo76953	AB543981	AB543993
Sagamilepeta sagamiensis (Kuroda and Habe, 1971)	Off Hota, Chiba Pref., Japan, 200–270m depth.	NSMT-Mo76954	AB543982	AB543994
PECTINODONTIDAE				
Bathyacmaea nipponica Okutani, Tsuchida and Fujikura, 1992	Japan	NUGB-Ba1	AB238588	AB543995
Pectinodonta rhyssa (Dall, 1925)	Off Kiishirahama, Wakayama Pref., Japan	NUGB-L428	AB238589	AB543996
Order COCCULINIFORMIA				
COCCULINIDAE				
Coccopigya punctoradiata (Kuroda and Habe, 1949)	Kamikawaguchi, Kochi Pref., Japan	NUGB-L266	AB238590	AB543997
Cocculina sp. A	Kumanonada, Mie Pref., Japan	NUGB-L429	AB238591	AB543998
Cocculina sp. B	Tosa Bay, Kochi Pref., Japan	NUGB-L617	AB238592	AB543999
Order VETIGASTROPODA				
FISSURELLIDAE				
Emarginula foveolata fujitai Habe, 1953	Seto Inland Sea, Hiroshima Pref., Japan	NUGB-L277	AB238593	AB544000
Emarginula variegata A. Adams, 1852	Benoki, Okinawa Pref., japan	NUGB-L348	AB238594	AB544001

Abbreviations Used in Text:

AGT – Agassiz trawl; MNHNCL – Museo Nacional de Historia Natural de Chile, Santiago; SEM – scanning electron microscopy; SMNH – Swedish Museum of Natural History; ZSM – Zoologische Staatssammlung, München

SYSTEMATICS

Family Lepetidae Gray, 1850

Remarks: This family contains species living in deep or cold waters. They live on pieces of old shells or on rocks, where they feed on precipitated detritus or, in shallow water, encrusting diatoms. Shallow water species occur only in high latitudes. The species of the family are most safely recognized by the radular morphology with a central complex of 4–6 sturdily built teeth and two feather-like ones on each side of the complex. The absence of ctenidium and secondary gills and the presence of well-developed oral lappets are more noticeable external characters, but these are not fully diagnostic, since they are shared with Neolepetopsidae. The shell usually has a better-defined sculpture of radiating ribs, often equipped with small scales or spine-like processes, when compared to other patellogastropods, but this is also shared with the Neolepetopsidae. Neolepetopsids, however, have a well-developed, perfectly transparent inner shell layer.

Species of Lepetidae are generally supposed to lack eyes, as indicated by their vernacular name "blind limpets", but this is not correct. Both *Iothia emarginuloides* and the type species *I. fulva* have very small black, pigmented eyes, situated on the tentacle bases, close to the head, having a diameter of 50–60 µm. According to Angerer and Haszprunar (1996: 173), they are supposed to be non-pigmented, but this is true only for *Lepeta caeca* (O.F. Müller, 1776) and *Propilidium ancyloides* (Forbes, 1840), among the species they investigated. The presence of eyes, however visible only in dorsal view, was confirmed both in *I. fulva* and in Chilean and Antarctic specimens of *I. emarginuloides*.

Generic level names included in Lepetidae: *Lepeta* Gray, 1847; *Propilidium* Forbes and Hanley, 1849; *Iothia* Forbes, 1849; *Cryptobranchia* Middendorff, 1851; *Sagamilepeta* Okutani, 1987; *Maoricrater* Dell, 1956; *Bathylepeta* Moskalev, 1977, and *Limalepeta* Moskalev, 1977. We are not convinced that all these generic names are needed to reflect the phylogeny of the family, but will refrain from making changes in their nomenclatural status at this point.

Genus *Iothia* Forbes, 1849

Type Species: *Patella fulva* O.F. Müller, 1776

Remarks: Species of this genus often have a shell with a distinctly yellowish or reddish color (Figure 9), but white or colorless shells also occur. The sculpture consists of distinct, scaly radial ribs, the apex is situated at the posterior third, and they have a distinctly convex posterior slope. Species have been reported from the North Pacific, North Atlantic, Antarctica, South America, and New Zealand (in this latter location as *Maoricrater* Dell, 1956).

Eight names have been used for species of Lepetidae in Antarctica and southern South America: **1.** *Patella albescens* Philippi, 1846 was placed in *Iothia* by Valdivinos (1999) and Forcelli (2000), but this species was described from "the shores in Central Chile" by Philippi (1846) and the description seems to be based on a young nacellid (Pilsbry, 1891: 36). The name has not been in modern use for any nacellids (Valdovinos and Rüth, 2005; Devries, 2008; De Aranzanmendi et al., 2009; González-Wevar et al., 2010), and is not discussed below; **2.** *Patella* (?) *emarginuloides* Philippi, 1868; **3.** *Tectura* (*Pilidium*) *coppingeri* (E.A. Smith, 1881); **4.** *Lepeta antarctica* E.A. Smith, 1907; **5.** *Propilidium pelseneeri* Thiele, 1912: 186, from the "Gauss Station" (68°S, 090°E), near Drygalski Island, Davis Sea; holotype in the Natural History Museum, Berlin, Mol 63.050; not seen; **6.** *Lepeta depressa* Hedley 1916: 42, from off the Schakleton Ice shelf in 220 m depth, has not been identified later. It was based on a single broken shell; not discussed below; **7.** *Pilidium fulviformes* Egorova, 1972; **8.** *Iothia coppingeri magellanica* Linse, 2002.

Bathylepeta is another lepetid genus with two species known from abyssal depths off Chile and in the Weddell Sea (ca. 5000 m). They differ by being quite large (25–30 mm) and having an almost smooth shell with central apex. One of them, *B. linsae* Schwabe, 2006 is included in the phylogenetic analysis.

Iothia emarginuloides (Philippi, 1868)
(Figures 5–6, 16–18, 23–26)

Patella (?) emarginuloides Philippi, 1868: 224. Type locality: "Magallanes, Potissimum Magellanicum [Magellan Strait], communicated by G. Acton". Type material: Museo Nacional de Historia Natural de Chile. Gueglielmo Acton was a Captain in the Neapolitanian Navy (Malakozoologische Blätter (1856) 3: 197). Transferred to *Iothia* by Pilsbry (1891: 72, as *Pilidium emarginuloides*.

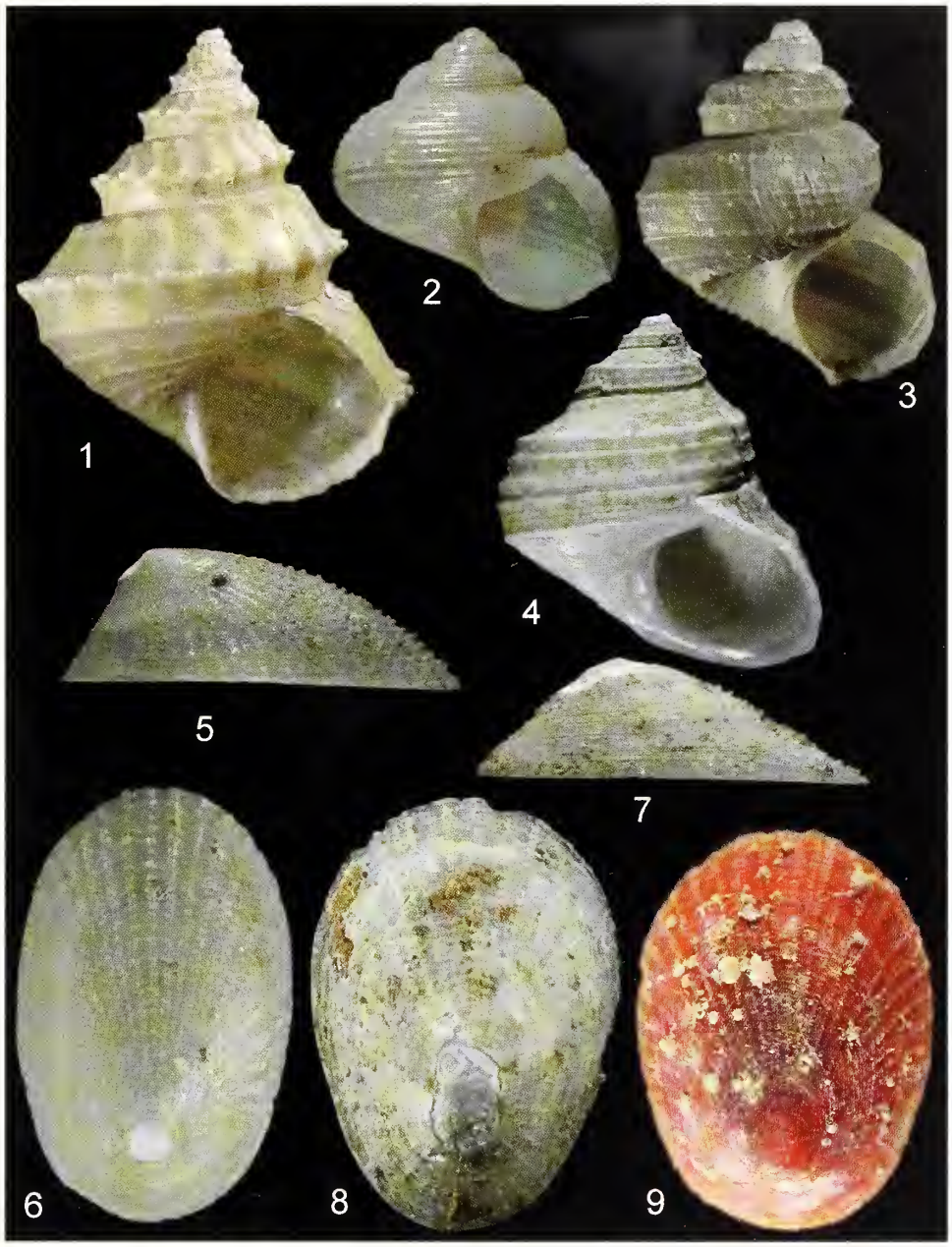
Tectura (Pilidium) coppingeri E.A. Smith, 1881: Type locality: Eastern part of Magellan Strait, 16–18 m depth. Holotype: Natural History Museum, London, not examined. Transferred to *Iothia* by Pilsbry (1891: 72) as *Pilidium coppingeri*.

Lepeta (Pilidium) antarctica E.A. Smith, 1907: 12. Type locality: Hole 10 (McMurdo Sound), 130 fathoms. Holotype: Natural History Museum, London, not examined. Considered a synonym by Hain (1990: 37), validity questioned by Schwabe (2006: 43).

Pilidium fulviformes Egorova 1972: 384. Type locality: Davis Sea, 15 m depth. Type material: P.P. Shirshov Institute of Oceanology, Moscow. Synonymized with *Iothia coppingeri* (Moskalev 1977: 62)

Iothia coppingeri magellanica Linse, 2002: 62. Type locality: Beagle Channel (Chile and Argentina) 55° 07.30′ S, 66°52.78′ W, 25 m depth. Type material: Zoological Museum, Berlin.

Material Examined: SMNH 102837, Chile, Golfo de Ancud, 42°26.4′ S, 072°59.0′ W, 250–300 m, 3 specimens (Lund University Chile Expedition); SMNH 103289, Lazarev Sea, 70°19.0′ S, 003°16.3′ W, 191–204 m, 5 specimens; SMNH 103290, Lazarev Sea, 69°59.4′ S, 008°00.3′ E, 161–161 m, 2 specimens; SMNH 103291, Lazarev Sea, 69°57.4′ S, 005°04.2′ E, 210–210 m, 1 specimen; SMNH 103292, Lazarev Sea, 70°24.2′ S, 006°08.1′ E, 118–126 m, 1 specimen; SMNH 103293, Lazarev Sea, 70°19.0′S, 003°16.3′ W, 191–204 m, 1 specimens; SMNH 103561, Chile, Magellan Strait, Punta Arenas, 13–15 m, 1895-12-04, Swedish Magellans Exp 1895-7#390, 2 specimens; SMNH 103562, Chile, Magellan strait, Romanche Bay, 21–27 m, dead shells on black clay (smooth, var. radiata Strebel), Swedish Magellans Exp 1895-7#665, 1 specimen; SMNH 103563, Chile, Magellan Strait, Punta Arenas, shell gravel, 27 m, Swedish Magellans Exp. 1895 #465, 1 specimen; SMNH 103564, Chile, Magellan Strait, Romanche Bay, 20 m, Swedish Magellans Exp. 1895-7#665, 2 specimens; SMNH 103689, Falkland Islands, Albermarle Harbour, 18–30 m, Swedish Antarctic Expedition 1901#57, 4 specimens;SMNH 103690, Chile, Otway Water, Puerto Toro, 1908-04-15, 20–30 m, Swedish Magellans Exp 1895-7#16, 2 specimens (smooth); SMNH 103936, Chile, off Concepción, 36°22.01′ S, 073°43.10′ W, 764–843 m, Leg Sellanes VG-07-AGT10, 1 specimen; SMNH 103867, Argentina, Tierra del Fuego, Beagle Channel, Bahia Lapataia, 54°51.5′S, 068°33.1′ W, 15–18 m, Leg. Diego



Figures 1–9. Gastropoda from Concepcion seeps, unless otherwise stated. **1.** *Bathybembix macdonaldi*, shell height 44.5 mm. **2.** *Margarites luloti*, shell height 23 mm. **3.** *Zetela alphonsi*, height 10.5 mm. **4.** *Cantrainea panamense*, shell height 21.8 mm. **5–6.** *Iothia emarginuloides*, length 5.8 mm. **7–8.** *Iothia megalodon*, holotype #6617, length 8.9 mm. **9.** *Iothia fulva*, Norway, Raunefjord, 50 m depth, length 5.7 mm.

Zelaya, 5 specimens, DNA extracted; ZSM Mol 20013014, Antarctica, 71°06.27′ S, 012°50.46′ W, 728–743 m , 1 specimen; ZSM Mol 20013011, Antarctica, 63°07.52′ S, 59°25.43′ W, 782 m, 1 shell; ZSM Mol 20013012, Antarctica, 71°06.27′ S, 012°50.46′ W, 728–743 m, 1 specimen.

Distribution: Antarctic circumpolar, the Subantarctic Islands and southern South America, north to Concepcíon (Chile), southernmost Argentina, the Falkland Islands, Kerguelen and Crozet Island (Dell, 1990; Linse, 2002; Aldea, Olabarria, and Troncoso, 2008), usually in 20–200 m depth.

Remarks: Supported by the fact that type specimens are very similar and were described from nearby localities (separated by maximum 400 km at the same latitude), we consider, as did Strebel (1907: 112), that *coppingeri* and *emarginuloides* are synonyms, and the consequence is that Philippi's name is the one to be used. Strebel

(1908), Egorova (1972), and Dell (1990) recognized this, but gave no reasons for their continued use of *coppingeri*. Philippi (1868) described the species as being similar to those in the genus *Emarginula*, but lacking gills. He also noticed that eyes were present in a specimen with dried soft parts, soaked in water. Both Chilean and Antarctic specimens have, contrary to common belief, small eyes, of 50–60 µm diameter, and visible only in dorsal view. In alcohol-preserved specimens, the eyes remain visible also after at least 100 years.

Schwabe (2006) reviewed some of the names supposed to be based on southern Lepetids, but did not change nomenclature.

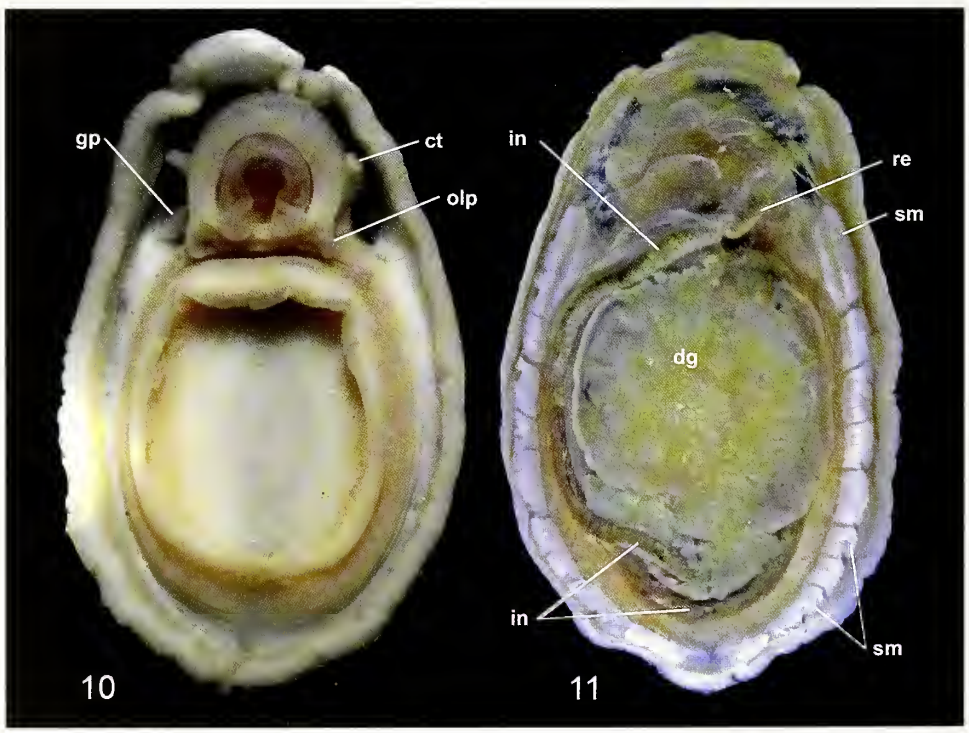
Iothia coppingeri magellanica Linse, 2002 was described as new because its radula was said to differ from Hain's (1990) pictures of the radula of *coppingeri* by having two instead of a single feather-like marginal tooth. Linse also says there is only a single southern species of *Iothia*, viz. *I. coppingeri*. *Lepeta antarctica*, *Iothia emarginuloides*, *Lepeta depressa*, and *Pilidium fulviformes* are not mentioned. Linse has compared the teeth of her Magellanic specimens and found them to differ from the "high-Antarctic *Iothia coppingeri*". However, *Iothia coppingeri* is no more "high-Antarctic" than Linse's *magellanica*; if anything, *I. coppingeri* is more northern since it was described from the Strait of Magellan, not from Antarctica. It is obvious from Egorova's (1972) drawings and Hain's (1990) SEM pictures that Antarctic specimens of *Iothia* have two featherlike teeth. If there had been differences as assumed by Linse, the Antarctic specimens would be the ones in need of a new name, but for them the name *antarctica* E.A. Smith, 1907 is available. Linse also stated (2002: 64) that her specimens could not be distinguished from *coppingeri* by shell morphology. Examination of the radula of a Chilean specimen and a specimen from Hain's collections in the Weddell Sea (partly kept in SMNH) did not show any obvious differences. The shells can usually be distinguished by the Antarctic specimens having a more vitreous shell but this is probably a result of the physical conditions when the shells were formed. We attempted to solve the problem by sequencing Antarctic specimens but no specimens available to us yielded a sequence.

If the Antarctic specimens are considered a distinct species, *Iothia antarctica* (E.A. Smith, 1907) is available for them (Zelaya, 2005).

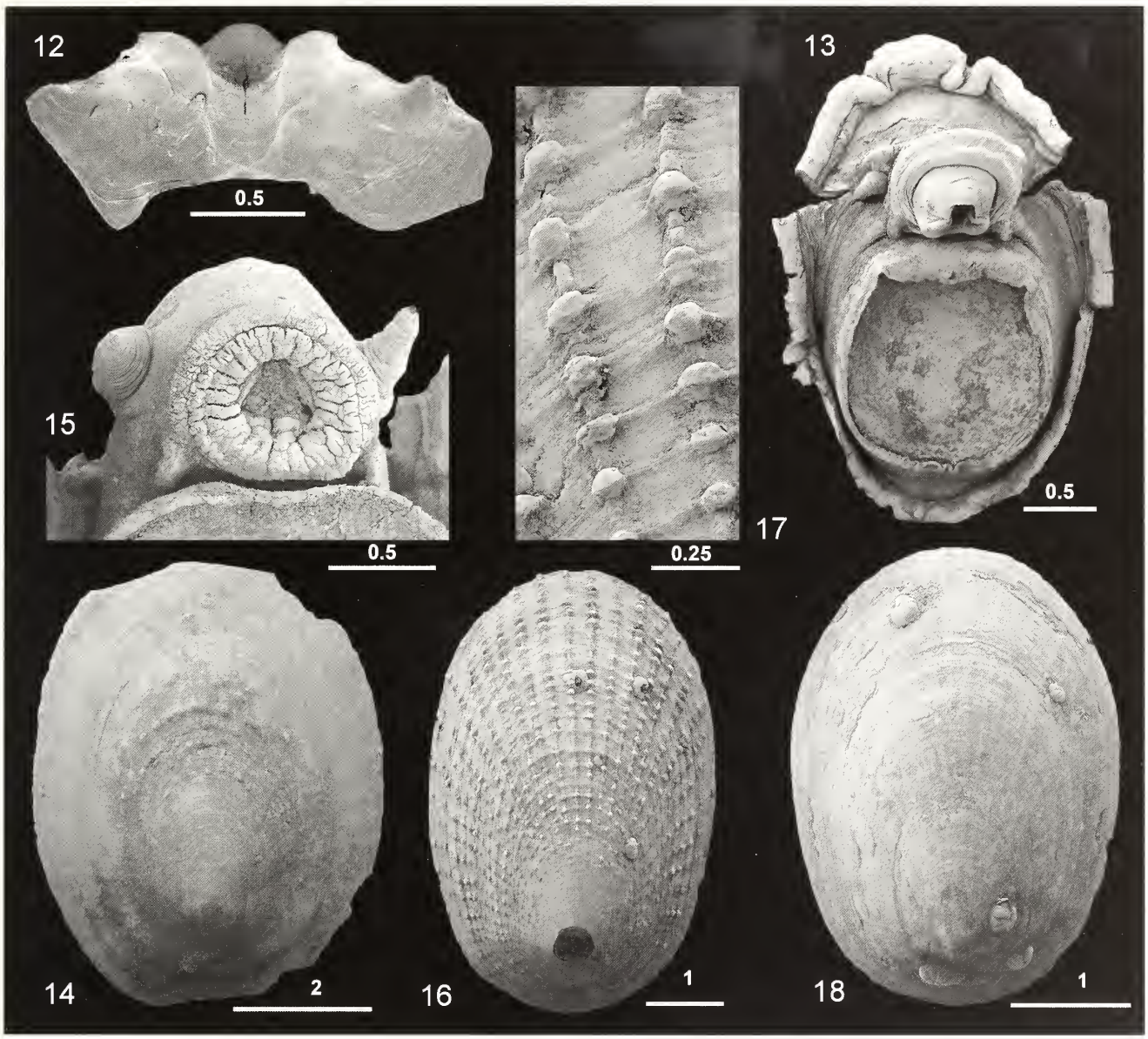
Specimens from shallow water in the Magellan Strait often have an almost smooth shell (Figure 18), only indications of the ribs remain. Such specimens look very different from large Antarctic and deep water specimens, which are invariably sculptured (Figure 16).

Iothia megalodon new species
(Figures 7–8, 10–11, 12–14, 19–22)

Description: Shell (Figures 7–8, 14) limpet-shaped, thin, flat, dirty yellowish white. Protoconch unknown. Sculpture of 45–50 radiating ridges made more distinct by a series of low spines, knobs, or blisters on each. Apex situated at or just behind the anterior 1/3, height of shell



Figures 10–11. *Iothia megalodon*, holotype. **10.** Ventral; **11.** Dorsal view of soft parts. Length of body 7 mm. et, cephalic tentacle; dg, digestive gland; gp, genital papilla; in, intestine; olp, oral lappet; re, rectum; sm, shell musele.



Figures 12–18. 12–14. *Iothia megalodon*. **12.** Jaw, inside, right side damaged. **13.** Body, critieal point dried. **14.** Shell, paratype 6618, unusually smooth. **15.** *Iothia fulva*, head. **16–17.** *Iothia emarginuloides*, shell and detail of sculpture of strongly sculptured specimen from the type locality of *I. megalodon*. **18.** *Iothia emarginuloides*, Almost smooth specimen, SMNH 102837, from Chile, Golfo de Aneud, 250–300 m depth. Radula of this specimen, see Fig. 25, H. Scale bars in mm.

1/3 of length. Periphery of base maximum breadth ea. 72% of length and situated at posterior 2/5. Maximum shell length known 9.9 mm.

Soft Parts (Figures 10–11, 13): Pallial furrow and cavity shallow, the latter with conspicuous anal and genital papillae above right eephalic tentacle. Cephalic tentaeles short, cylindrieal, lacking any external trace of eye. Snout large with ventral mouth, posterior eorners drawn out to small obtuse flaps. Gill absent.

Radula (Figures 19–22): Formula 2–2–0–2–2, not excessively long, 35 times as long as broad, length eorresponding to 70% of length of shell. Posterior third with poorly developed teeth; middle third with normal lepetid type teeth, anterior third with ca. 25–30 teeth with very large, "inflated bases"; "median tooth" with a single large and smooth cusp, obviously formed by tooth 2 from both sides of the radula, while the original central tooth is reduced or invisibly ineorporated. Second lateral tooth with two blunt denticles, possibly formed by fusion of teeth number 3 and 4 in other speeies of Lepetidae. Uneini soft and pliable, diffieult to spread apart; outer one larger than inner one; margin of apical part smooth (Figure 22). Jaw very sturdily built (Figure 12).

Figures 19–26. Radular morphology. **19–22.** *Iothia megalodon*, holotype, 8.9 mm. **19.** 2.5 mm of the transitional zone. **20.** Transition to large teeth. **21.** Detail of radula, tilted backwards to show borders between teeth. **22.** Tips of feather-like marginals. **23–24.** *Iothia emarginuloides*, Concepcion, figured in Fig. 16 (shell 5.5 mm). **23.** Two rows in vertieal view. **24.** Teeth tilted backwards to show demarcation. **25–26.** *Iothia emarginuloides*, Golfo di Aneud, SMNH 102837, (figured in Fig. 18, 4.5 mm). **25.** Two transverse rows in vertical view. **26.** Teeth tilted forwards to better show the feather-like structure of the two pairs of marginal teeth. Numbers on teeth or parts of teeth are counted with a hypothetical rhachidian as number 1. Scale bars in μm.

Type Material: Holotype, #6617 and 2 paratypes # 6618 and 6619 in MNHNCL; 5 paratypes SMNH type collection 6784, 7932, 7933 (for details see Materials and Methods).

Type Locality: Chile, methane seep off Coneepeión, 36°22.01′ S, 73°43.10′ W, 764–843 m.

Etymology: From *Carcharocles megalodon* (Agassiz, 1843), a fossil shark known from its large teeth.

Remarks: Differenees in soft parts separate *megalodon* from *emarginuloides*: absenee of eyes, abnormally large radular teeth in *megalodon* and the edge of the marginal teeth (uneini) being almost smooth in *megalodon*, not featherlike as in *emarginuloides* (Figures 23, 26). Additionally, the shell of the new speeies differs by being more depressed, having a less overhanging apex, and a pear-shaped eircumferenee instead of elongate and regularly ovate. The presenee of normal specimens of *Iothia emarginuloides* in the same trawl eateh suggests that *megalodon* is not a loeal form.

The radular type, with enlarged, shield-like teeth on the anterior third (Figure 19) is unique. The mineralized part of the normal lepetid radula ean be recognized in Figures 23 and 24 (*I. emarginuloides*), and is marked 2–4. These parts are assumed to correspond to three lateral teeth, whereas the raehidian tooth has been lost. They are attaehed to the radular membrane and are easily detached. The eorresponding parts in *I. megalodon* (Figures 20–21, numbered 2–4) are also easily detached, but leave intaet the whole shield-like area they are attaehed to. We eonsider this as an indiea-tion that the "shield" is formed by the basal membrane. The slender marginal teeth (or uneini, if one wants to refrain from homologizing) reaeh from the basal membrane to the tip of tooth 2 in lepetids in general; so they do also in *I. megalodon*, both before and after the development of the shield.

The loss of the raehidian tooth and fusion of the first lateral tooth from the two sides is obvious when the teeth are tilted baekwards (Figures 21, 24). So is also the fusion of teeth number 3 and 4 in *Iothia emarginuloides* (Figure 24), while this is not obvious in *I. megalodon* (Figure 21).

Iothia megalodon usually had the gut full of white ealeareous matter, sometimes with seetions of the gut filled with grey sediment and mineral particles, and is evidently seraping off sediment from the shells and carbonate rocks where it lives. As in patellogastropods in other seep localities, the gut eontent oeasionally was unexpectedly rieh in radiolarian fragments.

DISCUSSION

Biotope and Fauna

A limited number of mollusk species regularly show up in vent or seep loealities, often in high numbers and eoncentrated around the souree(s) of effluents. They are usually distributed along or within a certain geologic structure, like a mid-ocean ridge, a coastline, or a series of seamounts. Their numbers invariably drop drastically to zero only a short distance from the souree of the effluents. Among the bivalves, many have symbiotic bacteria (reviewed by Sibuet and Olu, 1998). Among gastropods, only a few have such associations but those that have are large and conspieuous (Warén and Bouchet, 2001) and are only known from vents. For the symbiotie species, it is not difficult to understand that they are vent/seep dependent, or favored by the presence of the effluents needed by the symbionts.

The vast majority of the vent/seep gastropods are grazers that utilize the rieh bacterial growth on all surfaces, as well as material precipitated from the water (Warén and Bouchet, 1993, 2001, 2009). Among the seep gastropods, a few bueeinids are scavengers and several species of the Conoidea, mainly belonging to the genus *Phymorhynchus*, are active predators. They can be assumed to profit from the mneh elevated biomasses (e.g., Levin and Michener, 2002).

The genera containing species favored by seeps are often distributed all over the world and their number is quite limited, about 25–30 "seep gastropod genera" (Warén and Bouehet, 1993, 2001, 2009; Sasaki et al., 2010). The proportion of these that is present at a given seep site is a good indication if it is a rich or poor seep fauna. More than half of them are present in the very rieh seeps off the Paeific coast of Costa Rica (Warén unpublished).

Most of the vent/seep gastropod species are adapted to their environment by having different forms of haemoglobin as oxygen earrier or in simplifieation of the shell. Vent/seep speeies are rarely found outside the vent-seep sites, although Johnson et al. (2007) found a eouple of speeies believed to be vent endemics on, sunken drift wood 2000 km north of the nearest vent where it is known to oeeur. The vent/seep species are often called "vent/seep-dependent" (Sibuet and Olu, 1998) even if the degree of dependency has not been quantified, and perhaps they should better be termed "favored by vents and seeps".

The main reason for our difficulty in recognizing the vent-seep eomponents of the fauna is probably laek of knowledge of the fauna outside the seeps, whieh is more diverse, albeit poorer in specimens. As a rule of thumb, when visually directed collecting (manned submersibles, Video-monitored-grabs, or ROVs) is used in vents or seeps, the vast majority of the recovered specimens belong to the vent-seep fauna.

About 22 speeies of gastropods have been considered characteristie of the seep biota off Concepción (Sellanes, Quiroda and Gallardo, 2004; Sellanes et al., 2008, and listed below), whieh so far only have been explored by trawling and reeently by TV-directed tube-coring (L. Levin, pers. eomm).

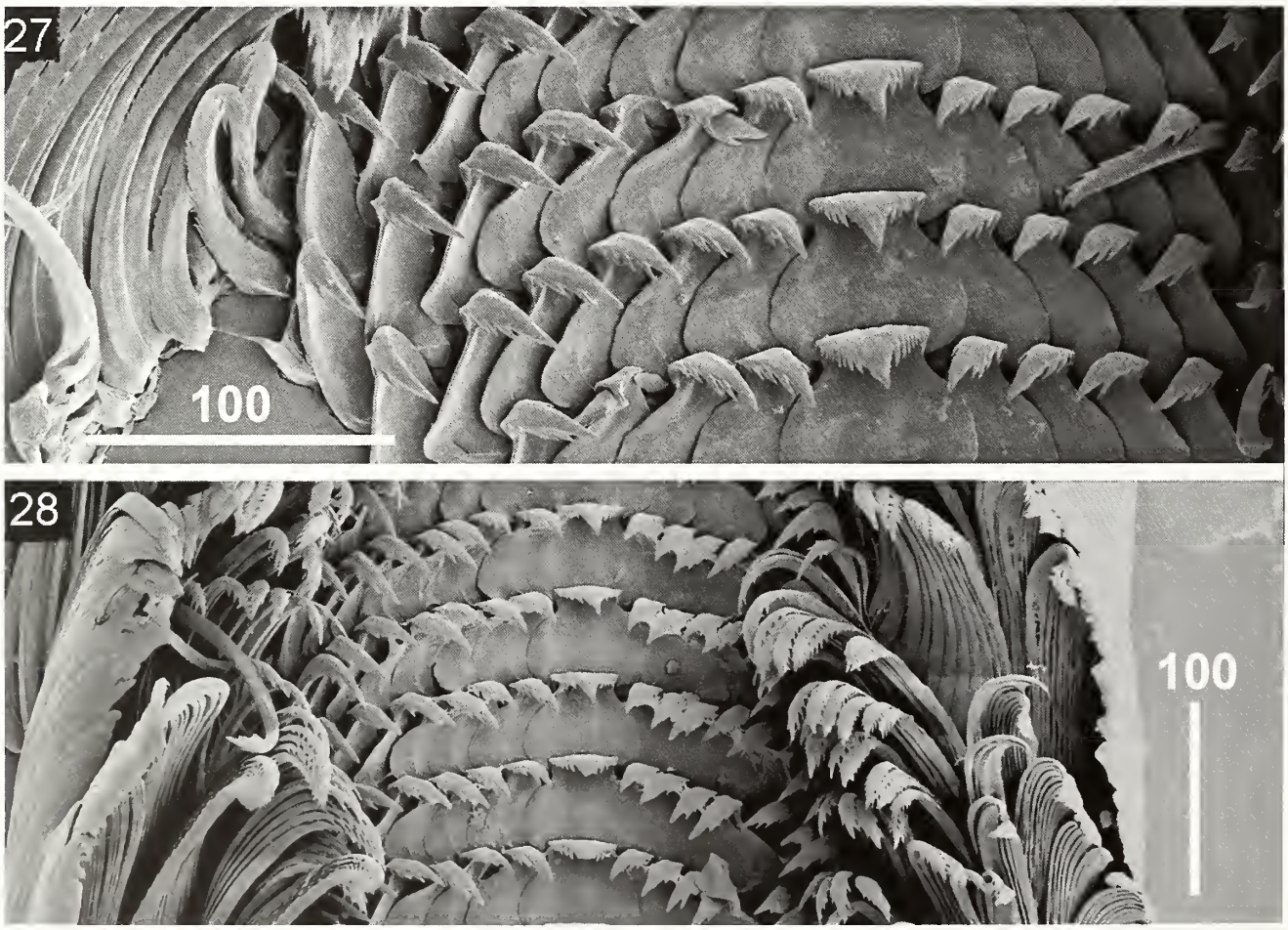
Several genera of gastropods known to be eommon in seeps have not been found in the Chilean seeps, some of them perhaps beeause of their small size (species of *Hyalogyrina*, *Cima*, *Xylodiscula* ≈ 1–2.5 mm). Others

are of sizes similar to those of the known fauna (species of *Provanna*, *Paralepetopsis*, *Phymorhynchus*, and *Lepetodrilus* ≈ 6–20 mm), and are more likely to have been collected also with the limited resources at hand, if they were present. However, they may still be present since the site may not have been completely collected although a total of 13 trawls are believed to have passed across the seeps or their immediate neighborhood. During the French exploration of the seeps off West Africa (Warén and Bouchet, 2009), six hauls with a 5 m beam trawl and intensive sieving and search of the catch (von Cosel, pers. comm.), recovered only 4 out of 8 seep gastropod genera present at the site. The mesh of a trawl, in this case 10 mm, does not exclude smaller species; sediment is almost always caught and clogging the net, which then retains also small organisms.

Accompanying Gastropod Fauna

Margarites huloti Vilvens, 2006 (Family Trochidae) (Figures 2, 27–28) is not easily classified on shell characters alone and its radula is therefore figured (Figures 27–28). It is similar to that of species of Gazini (Trochidae). Few Gazini radulae have been figured but Hickman and McLean (1990: fig. 53) figured an unidentified species and *Gaza superba* (Dall, 1881), and Simone and Cunha (2006) reviewed the group. Species of *Margarites* and the Antarctic sister group *Margarella* have 4–6 lateral teeth, species of Gazinae have more, 7–8 laterals. Species of *Gaza* are sometimes common around carbohydrate seeps in the Gulf of Mexico (Warén and Bouchet, 1993, 2001). At present, there seems to be no generic name published for a genus where *M. huloti* fits, so we leave it in *Margarites*. The gut contained sediment in two specimens which were examined. Similar species are known from Japanese seeps and vents (*Margarites ryukyuensis* Okutani et al., 2000 and *M. shinkai* Okutani et al., 1992) and from the Manus Basin (Warén, unpublished) and we feel confident that this is a species adapted to and favoured by the seep environment.

Iothia emarginuloides (Philippi, 1868), *I. megalodon* new species (Lepetidae). Very similar, undescribed species are known from seeps in the Gulf of Mexico, off western Costa Rica, and off Oregon (Warén, unpublished). Therefore, we group *L. megalodon* as a seep species, while *I. emarginuloides*, which is mainly



Figures 27–28. *Margarites huloti*, radular morphology. **27.** Central Field. **28.** Whole width of radula. Scale bars in µm.

known from non-seep environments, probably is an occasionally occurring intruder.

Puncturella, (Family Fissurellidae). Two species found (Sellanes, unpublished) at Concépcion. Species of Fissurellidae seem to be regularly occurring in the outskirts of vents and in seeps, but they seem to be local species and no biotope specific radiation has been recognised, from seeps, vents or wood (Warén and Bouchet, 2009).

Cantrainea panamense (Dall, 1908) (Family Turbinidae (Colloniinae)) (Figure 4). May be a sister species to *Cantrainea macleani* Warén and Bouchet, 1993 described from Caribbean seeps (see also Garciá and Lee, 2002), since they are more similar to each other than to any other known Colloniinae. Species of *Cantrainea* are also known from Japanese hydrothermal vents (*Cantrainea jamsteci* (Okutani and Fujikura, 1990) and *C. nuda* Okutani, 2001) and fossil seeps in Japan (Kaim, pers. comm.). Several species of Colloniinae, including *C. panamense,* are also common on woodfalls (Warén, unpublished). From phylogeny and records, we consider this as a species with seep affinity.

Zetela alphonsi Vilvens, 2002 (Family Solariellidae) (Figure 3). Species of Solariellidae are occasionally found in cold seeps, sometimes more than single specimens, but no biotope specific radiation has been recognized and there is no indication of a solariellid species to be endemic to seeps. Therefore we believe this to be an occasional intruder.

Calliostoma chilena Rehder, 1971; *Calliostoma crustulum* (Vilvens, 2006) (Family Calliostomatidae). Species of Calliostomatidae are usually associated with sponges or hydroids and their occurrence may be related to occurrences of these. No radiation of calliostomatids has taken place in vents and seeps and no species of Calliostomatidae is known to be vent or seep dependent or even regularly occurring there.

Bathybembix macdonaldi (Dall, 1890) (Family Calliotropidae) (Figure 1). The distribution of the more northern relative *Bathybembix bairdii* (Dall, 1889) was reviewed by Hendrickx and Lopez (2006). Species of *Bathybembix* occur regularly in cold seeps, often in considerable quantities (Warén and Bouchet, 2001, 2009). The overview of these large calliotropids is obscured by the multiplication of generic names like *Gincbis* Noda, 1975, *Lischkeia* Fischer, 1880, *Bathybembix* Crosse, 1892, and *Bembix* Watson, 1879. These are all quite similar in shell and radular morphology and most likely closely related. This seems also to be the case with the fossil genus *Amberleya* Morris and Lycett, 1850, which comes close to *Lischkeia*, at least species like *A. dilleri* Stanton, 1895 and *A. morganensis* (Stanton, 1895), which occurred in a Late Jurassic to Lower Cretaceous seep environment along the North American West Coast. Kiel et al. (2008) drew the attention to this similarity, as well as to *Eucycloscala* Cossmann, 1895 and *Eucyclus* Eudes-Deslongchamps, 1860, and Janssen (1993) used the name *Bathybembix* for German Oligocene specimens. A careful comparison, based on molecular methods where possible, is needed to better understand the relations among these groups.

Calliotropis cceliae Vilvens and Sellanes, 2010 (Family Calliotropidae). One species of *Calliotropis* was reported from West African methane seeps (Warén and Bouchet, 2009) and AW has seen other species of *Calliotropis* from seeps in the Philippines and off Taiwan (unpublished). Species of *Calliotropis* invariably have their gut filled with sediment (Warén, unpublished), and are likely to gain from the rich bacterial growth. We therefore consider their presence indicative of seep environment and that they should be called "seep species" (althogh most species of the genus inhabit the normal deep-sea).

Caenogastropoda. The large species of predatory and scavenging Caenogastropoda are probably attracted by the increased biomasses and occurrence of possible prey. Here belong: Naticidae ("*Natica* sp.") Ranellidae (*Fusitriton magellanicus* (Röding, 1798)), Muricidae (*Trophon ceciliae* Houart, 2003; *Trophon condei* Houart, 2003; *Trophon* sp.; and *Pagodula concepcionensis* Houart and Sellanes, 2006), Buccinidae (*Kryptos explorator* Fraussen and Sellanes, 2008), Volutidae (*Miomelon philippiana* (Dall, 1890)), and the Conoidea (*Aforia* cf. *goniodes* (Watson, 1881) and two unidentified species of Conoidea).

Systematic Position of *Iothia*

The family Lepetidae is thought to be a sister group of the Acmaeidae and Lottiidae (Lindberg, 1988; Lindberg and Hedegaard, 1996), but anatomical characters such as the presence of a gill in Acmaeidae–Lottidae and the widely different radular morphology, separate Lepetidae from these families (Sasaki, 1998). Recent molecular work suggests that Lepetidae is closely related to Pectinodontidae and Nacellidae (Nakano and Ozawa 2007).

Moskalev (1977) reviewed the family Lepetidae worldwide and classified the species based on their radular characters. Later, Okutani (1987) proposed a new genus *Sagamilcpeta* primarily on radular features. Angerer and Haszprunar (1996) summarized the anatomy of *Lepeta*, *Iothia*, and *Propilidium*. According to Sasaki (1998), eight genera are currently recognized within Lepetidae, but their relations are poorly understood. Only a few representatives of Lepetidae have been analysed using molecular data until now (Harasewych and McArthur, 2000; Nakano and Ozawa, 2007).

To stabilize our generic concept, we used some sequences from an ongoing project on the phylogeny of the Patellogastropods in seeps and vents (Nakano and Warén, unpublished) for a preliminary and simplified analysis (Figure 29). Our study includes the species belonging to six named genera, including the type species, *Lepeta caeca*, *Limalepeta lima*, *Sagamilepeta sagamiensis,* and *Iothia fulva*. Unfortunately, we were not able to include the type species of *Propilidium* and *Maoricrater* but the letter is very similar to and probably a synonym of *Iothia*.

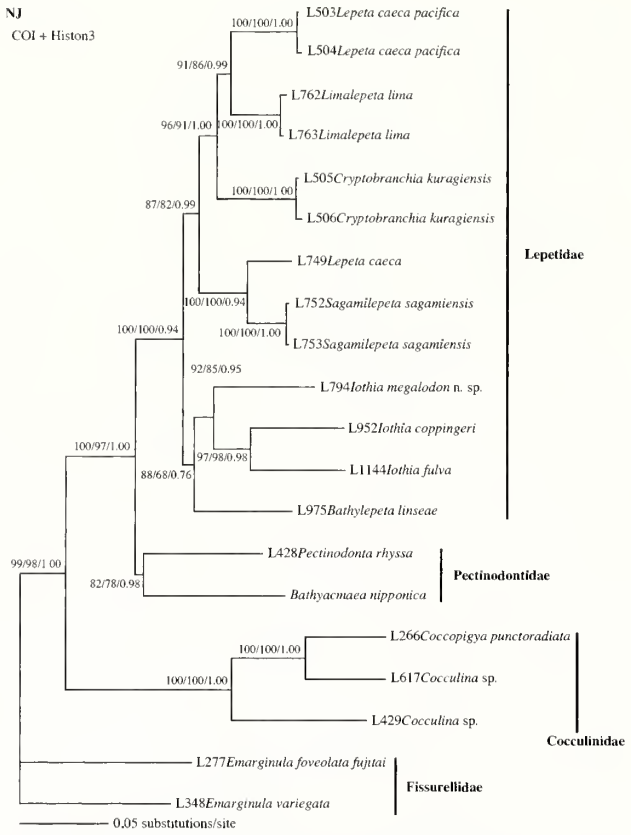


Figure 29. NJ phylogram generated from the 986 bp combined COI and Histone H3 data, showing NJ bootstrap, equally weighted MP bootstrap and Bayesian posterior probabilities.

The monophyly of Lepetidae is strongly supported (NJ=100%, MP=100%, PP=0.94) in the phylogenetic trees, as the results of Nakano and Ozawa (2007) suggest. This is also in agreement with the highly apomorphic radula which is quite uniform throughout the family. Two main elades are identified in the family Lepetidae eorresponding to *Iothia* plus *Bathylepeta* and the remaing the Lepetidae (*Lepeta*, *Cryptobranchia*, *Limalepeta,* and *Sagamilepeta*) (Figure 29).

The monophyly of the genus *Iothia*, as used here was supported by NJ=92, MP=85, and PP=0.95, and the position of the new speeies in *Iothia* thus seems well supported.

Further work will be needed to evaluate the subdivision of Lepetidae.

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Descriptions and illustrations of some new and poorly known turrids (Turridae) of the tropical northwestern Atlantic. Part 2. Genus *Crassispira* Swainson, 1840 subgenera *Monilispira* Bartsch and Rehder, 1939 and *Dallspira* Bartsch, 1950

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ABSTRACT

Notes, supplemental or new descriptions, and illustrations are provided for nine small, less than 10 mm in height erassispirine turrids in the genus *Crassispira* Swainson, 1840, subgenera *Monilispira* Bartsch and Rehder, 1939 and *Dallspira* Bartseh, 1950 of the tropieal northwestern Atlantic. Most are relatively unknown because of the unavailability of quality figures and adequate descriptions; one is previously undeseribed. This group has been a souree of confusion to workers attempting to identify material eollected in recent decades. Each is treated systematically, including synonyms, deseription, variability in form, distinguishing characteristics, and geographic range. Speeies in the subgenus *Monilispira* include *Crassispira mayaguanaensis*, new species, *C. latizonata* (E.A. Smith, 1882), *C. nigrescens* (C.B. Adams, 1845), *C. elatior* (C.B. Adams, 1845), *C. verbernei* de Jong and Coomans, 1988, *C. pellisphocae* (Reeve, 1845), and *C. guildingii* (Reeve, 1845). Species in the subgenus *Dallspira* inelude *C. flavocincta* (C.B. Adams, 1850), *C. fuscocincta* (C.B. Adams, 1850), and *C. bandata* (Usticke, 1969). A few notes are made regarding *C. fuscocincta*; however, this speeies is still an enigma beeause no speeimen has been aequired for comparative study.

Additional keywords: Gastropoda, Neogastropoda, lectotype designation

INTRODUCTION

This is the second in a series of papers covering relatively unknown or confusing small erassispirine turrids of the tropical northwestern Atlantic (TNWA). In this part, seven speeies in the subgenus *Monilispira* Bartseh and Rehder, 1939 are diseussed. These taxa share spiral sculpture, mostly tightly beaded, and numerous narrow axial ribs as the dominant sculptural element. Three speeies in the subgenus *Dallspira* Bartsch 1950 are also treated, eaeh possessing low broad ribs with peripheral nodules. My intention is to re-describe some poorly known speeies in these subgenera, to update their synonymies, and to elaborate on their zoogeography. Although most of these were described over 150 years ago, their obscurity at present is due to a number of factors: (1) deposition of types in the Natural History Museum (London), making them relatively inaccessible to American workers; (2) scarcity of specimens in museum colleetions; (3) relative inaccessibility of their habitats, whieh are prineipally in the shallows near the islands of the southeastern Caribbean; and (4) small size (less than 10 mm). Progress in bringing these species to the attention of the malaeologieal eommunity has been slow. Clench and Turner (1950) published previously un-illustrated photographs of C.B. Adams' types (*Pleurotoma nigrescens*, *P. elatior*, *P. flavocincta*, and *P. fuscocincta*). Maes (1983) visited the Natural History Museum (London) in the early 1980s for the purpose of examining type material and later expanded on the understanding of a turrid community in the British Virgin Islands. Among the taxa she treated that are also in this work are *Crassispira nigrescens* (C.B. Adams, 1845) and *C. pellisphocae* (Reeve, 1845). Shortly afterward, Kaicher (1984) published photographs of type material but of only one species treated here, *C. nigrescens*. In addition, mid- to late-twentieth century authors added new speeies from geographieally restricted areas. Nowell-Ustieke (1969) described *C. bandata* from St. Croix, and de Jong and Coomans (1988) described *C. mennoi* and *C. verbernei* from the Netherlands Antilles. Photographs of a great many turrid types have only reeently been made available (Williams 2005, 2006, 2009), including some types in the Natural History Museum (London) not previously published. These include the type of *C. latizonata* (E.A. Smith, 1882). *Crassispira mayaguanaensis*, new speeies, present in museum trays for decades is formally described for the first time. By presenting as many of the *Monilispira* and *Dallspira* as is possible at this time, the differential diagnoses can be better demonstrated.

MATERIALS AND METHODS

The methods and materials appearing in the first part of this series (Fallon, 2010) apply to this work. Specimens and types were examined at the National Museum of Natural History, Smithsonian Institution, Washington, DC (USNM), the Academy of Natural Sciences of Philadelphia (ANSP), and the Natural History Museum (London) (NHMUK) for this work. St. Vincent and the Grenadines is herein abbreviated SVG.

SYSTEMATICS

Subfamily Crassispirinae Morrison, 1966, *sensu* McLean, 1971a, b
Genus *Crassispira* Swainson, 1840

Type species: *Pleurotoma bottae* Kiener, 1839, a junior synonym of *Crassispira incrassata* (G.B. Sowerby I, 1834), by subsequent designation (ICZN, 1965).

Remarks: This genus has the largest number of species of all crassispirine genera. As a group they are heterogeneous for characters other than those that define the Crassispirinae and consistent in that they lack the combination of characters that narrowly define each of the other genera in the subfamily. Numerous subgenera have been erected to impose some order, and some have argued for the elevation of the subgenera to genus level (e.g., Kantor et al., 1997). The more traditional practice of including them all in *Crassispira* is followed here because subgeneric assignment is still provisional for many species. More research is needed on most members of this diverse group, and until the differences among the subgenera are more clearly defined, and perhaps new ones erected where necessary, it is felt more appropriate to keep them all under *Crassispira*.

Subgenus *Monilispira* Bartsch and Rehder, 1939

Type species: *Drillia monilifera* Carpenter, 1857 by original designation.

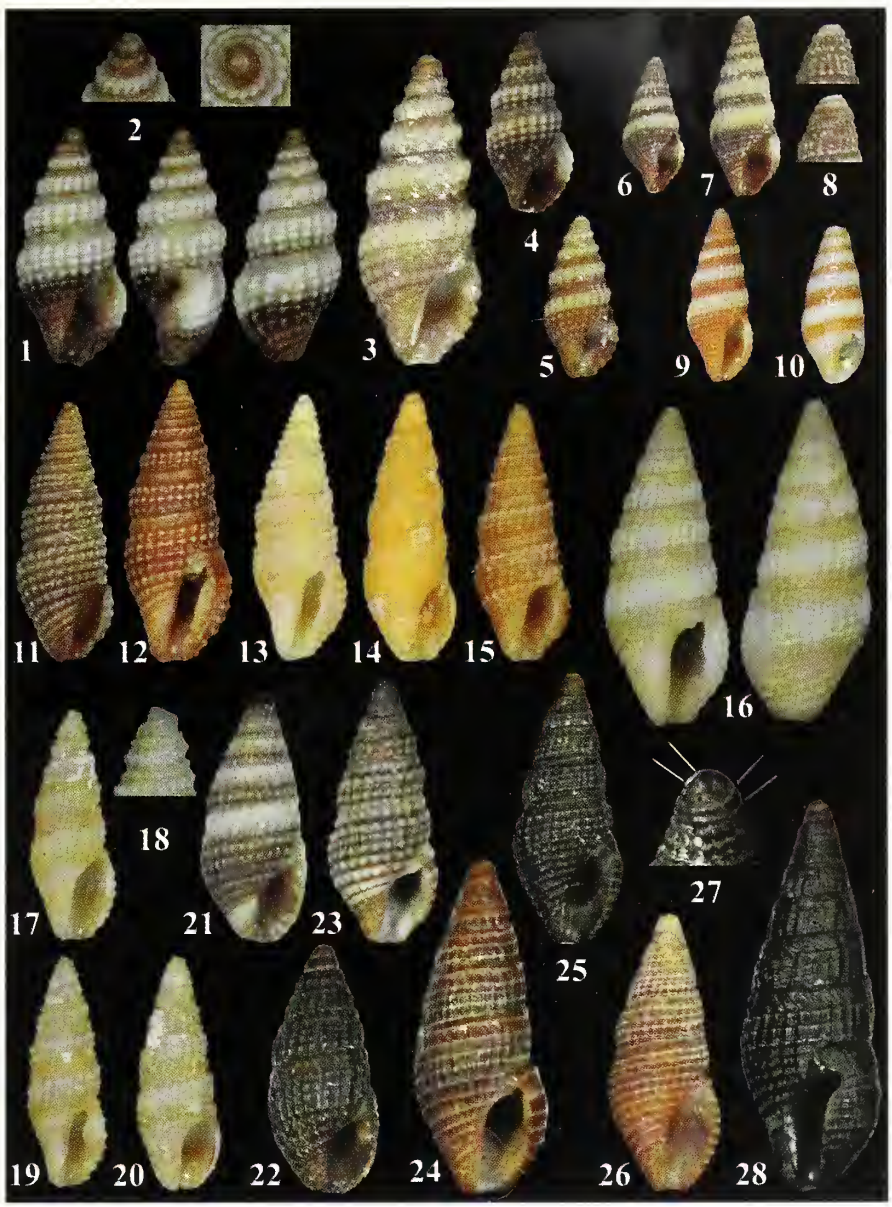
Remarks: Bartsch and Rehder's description of *Monilispira* originally included *Pilsbryspira monilis* (Bartsch and Rehder, 1939), which has a toxoglossate radula, unlike the crassispirine one (two marginal teeth only) of the type species (McLean, 1971a: 120–121). While their description of *Monilispira* could fit some *Pilsbryspira*, it is restricted in the TNWA to generally smaller, more tightly beaded crassispirines. According to Bartsch and Rehder (1939: 137), members of this subgenus have 2 smooth protoconch whorls, followed by a whorl of axial riblets. The teleoconch whorls have a strong subsutural cord and a row of nodules just above the whorl's periphery. The base of the shell has three nodulose spiral threads, and two more on the posterior portion of the columella. The entire surface of the shell has growth lines and spiral threads. The anal sinus is deep and lies on the shoulder between the suture and first row of nodules. Inner lip is reflected and appressed to the columella with a parietal callus at the junction of the inner and outer lips.

The *Monilispira* are distinguished, in most cases, by the dominance of spiral over radial sculpture, including a subsutural cord, peripheral beaded cords, additional beaded cords on the shell's base, and spiral threads in between. The type species, *M. monilifera* from the eastern Pacific, has a single peripheral row of beads, but TNWA species usually have multiple rows of beads on the whorls' periphery, and on the shell's base. However, the degree of beading is variable, even absent in *C. guildingii* (Reeve, 1845), which is provisionally placed in *Monilispira*. Also, TNWA species typically have only two protoconch whorls, the last one-quarter to one-half with axial riblets; anal sinus deep, U-shaped and in mature specimens may be partially constricted at its opening by the parietal callus.

Crassispira (*Monilispira*) *mayaguanaensis* new species
(Figures 1–4)

Crassispira latizonata auct. non (E.A. Smith, 1882): Williams (2005, 2006, and 2009: number 3105, right side photographs only) is likely this species. It was collected at 30 ft [9.1 m], Start Bay, Mayaguana I., Bahama Is. (Williams, pers. comm., 20 Jul 2009).

Description: Shell with 7 rectilinear whorls, stoutly fusiform, anterior half truncated. Whorls give shell a somewhat turreted appearance (Figure 1). Largest specimen examined 8.6 × 3.6 mm (Holotype 6.6 × 3.0 mm). Protoconch with 2 whorls, dome-shaped, smooth except for last one-third, which has 7 distinct, curved riblets (Figure 2). First teleoconch whorl with abrupt appearance of sutural cord and numerous white riblets with a central nodule, second whorl with fine threads that divide ribs into 2 rows of beads, and by third, 4 rows of round white beads that continue to last whorl. Shell base with 4 more beaded rows, last only weakly so; anterior canal with 5 plain spiral cords. Subsutural cord small, only a few diameters greater than spiral threads, lies very close to suture, and undulates with ribs beneath appressed suture. Sulcus (this feature just anterior to suture) with variably-spaced spiral threads made finely nodulous by curved intersecting growth striae, which mirror outline of anal sinus. Beaded rows separated by variable number of fine threads throughout. Closely spaced ribs number 19 on penultimate and 21 on body whorl, where they evanesce on shell's base. Outer lip thin, without a noticeable stromboid notch (a shallow one present on some in type series). Anal sinus lies just below subsutural cord, deep and U-shaped, slightly constricted by a projection of uppermost part of outer lip and parietal callus, causing sinus to appear diagonally oriented. Varix behind anal sinus composed of 3 swollen ribs; 2 additional ribs lie between varix and edge of outer lip. Inner lip thick, opaque, with a parietal callus at its junction with outer lip. Aperture narrow, but bowed out at its midpoint, ending in a short, open siphonal canal



Figures 1–28. *Crassispira* species. **1–5.** *Crassispira* (*Monilispira*) *mayaguanaensis* new species. **1.** Holotype, USNM 1150455, Abraham's Bay, Mayaguana I., Bahama Is., 6.6 × 3.0 mm. Ventral, lateral, dorsal views. **2.** Same specimen, two views of the protoconch. **3.** Paratype, ANSP 355561, Gold Rock, 20 mi [32.2 km] E of Freeport, Grand Bahama I., Bahama Is., 8.6 × 3.6 mm. **4.** Paratype, USNM 902238, Start Bay, Mayaguana I., Bahama Is. **5.** ANSP 368463, McLeans Town, Grand Bahama I., Bahama Is., 4.5 mm. **Figures 6–10.** *Crassispira* (*Monilispira*) *elatior* (C.B. Adams, 1845). **6.** USNM 502365, Pelican I., Barbados, 5.5 × 2.5. **7.** Same lot, 7.2 × 3.0 mm specimen. **8.** Enlarged view of protoconchs of two previous specimens. **9.** USNM 502364, Barbados, 6.9 × 2.8 mm. The light color of this beach-collected specimen may be due to exposure. **10.** ANSP 200027, E. Colon I., Bocas del Toro I., Panama, 4.4 × 1.9 mm. **Figures 11–15.** *Crassispira* (*Monilispira*) *nigrescens* (C.B. Adams, 1850). **11.** USNM 1150457, Limekiln Bay, Carriacou I., Grenada, 7.2 × 2.7 mm. **12.** Author's coll., Clifton Harbor, Union I., SVG, 7.8 × 3.0 mm. **13.** ANSP 349135, Oranjestad, Aruba, Netherlands Antilles, 7.4 × 2.7 mm. **14.** ANSP 350161, Fernando de Noronha Is., Brazil, 7.4 × 2.6 mm. **15.** Author's coll., San Blas Is., Panama, 7.1 × 2.6 mm. **Figures 16–20.** *Crassispira* (*Monilispira*) *latizonata* (E.A. Smith, 1882). **16.** Holotype, NHMUK 1874.5.26.88, locality unknown, 8.9 × 3.5 mm. **17.** USNM 1150458, Falmouth Bay, Antigua, 6.3 × 2.4 mm. **18.** Same specimen, enlarged view of protoconch. **19.** Author's coll., Falmouth Bay, Antigua, 6.4 × 2.5 mm. **20.** ANSP 350160, Fernando de Noronha Is., Brazil, 6.5 mm. **Figures 21–23.** *Crassispira* (*Monilispira*) *verbernei* De Jong and Coomans, 1988. **21.** ANSP 349132, Oranjestad, Aruba, ca. 4.8 × 2.1 mm. **22.** ANSP 349133, Oranjestad, Aruba, 4.7 × 2.1 mm. **23.** USNM 1150459, La Blanquilla I., Venezuela, 5.1 × 2.1 mm. **Figures 24–28.** *Crassispira* (*Monilispira*) *pellisphocae* (Reeve, 1845). **24.** Type, NHMUK 1879.2.26.43, locality unknown, 9.2 × 3.7 mm. **25.** Author's coll., Union I., St. Vincent and the Grenadines, 7.5 × 3.1 mm. **26.** Author's coll., Union I., SVG, 7.7 × 3.2 mm. **27.** Author's coll., Union I., SVG, protoconch of a 6.8 × 2.6 mm specimen. Lines indicate position of the two spiral cords. **28.** Author's coll., Cabo de La Vela, Columbia, 10.8 × 4.3 mm.

very slightly twisted to right. Shell color white, the 4 rows of closely-packed white beads most apparent, with a brown anterior that begins just below anterior-most beaded cord such that a thin brown line shows at suture of spire whorls. Color visible on interior of shell. Shell apex a lighter, golden brown.

Type Material: Holotype: USNM 1150455 (Figures 1–2). Paratypes: 2 spec., 8.6 × 3.6 (Figure 3) and 8.2 × 3.2 mm, Gold Rock, 32.2 km [20 mi] E of Freeport, Grand Bahama I., Bahama Is. (ANSP 355561); 1 spec. (Figure 4), at 9.1 m [30 ft], Start Bay, Mayaguana I., Bahama Is., G. Mackintosh! 24 Mar 1996 (USNM 902238); and 2 spec., 6.1 × 2.5 and 4.5 × 2.1 mm, Marina Bay, Providenciales, Turks and Caicos Is., M. Williams! 16 Aug 1981 (ANSP 357847).

Type Locality: Abraham's Bay, Mayaguana I., Bahama Is., in 12 m.

Material Examined: 5 spec., 3.6, 4.2 (tip broken), 4.5 (Figure 5), 4.9 (tip broken), and 5.8 mm, at 0 ft, McLeans Town, Grand Bahama I., Bahama Is., J. Worsfold! (ANSP 368463); 1 spec. 5.9 × 2.5 mm, from 24.7 m [81 ft], Gold Rock, Grand Bahama Is., Bahama Is. (ANSP 369725).

Distribution: All specimens examined are from the Bahama and Turks and Caicos Islands. The specimen figured in Williams (2005, 2006, 2009: number 3105, right side photographs only), which is this species, was taken at 9.1 m [30 ft], Start Bay, Mayaguana I., Bahama Is. (Williams, pers. comm., 20 Jul 2009). A specimen in USNM 935957 from Ascension Bay, Quintana Roo, Mexico has been identified as this species (Tippett, pers. comm., 19 Aug 2009). Its presence in the western Caribbean indicates a broader range.

Remarks: *Crassispira mayaguanaensis* has the typical characteristics of *Monilispira*: spiral sculpture dominant, beaded peripheral cords, lesser beaded cords on the shell base, and spiral threads (or grooves) present between the cords. From *Buchema primula* (Melvill, 1923) it differs in having round beads on its shoulder that are crowded together, not elongate spiral cord swellings as in *B. primula*. (*Buchema primula* is re-described in Fallon, 2010: 170.) There are more ribs, about 19 on the penultimate whorl, than on the equivalent whorl of *B. primula*, which has about 11. The whorl shoulders are squarish, not rounded as in *B. primula*. Although superficially similar to *C. latizonata* (E.A. Smith, 1882), this species has a smooth, domed-shaped protoconch, not the ridged, squarish one of *C. latizonata*. From *C. nigrescens* it differs principally in having a larger, more dome-shaped protoconch, square shoulders, not rounded ones, and in lacking a heavy subsutural cord.

Etymology: Mayaguana Island Crassispira. The species is named for Mayaguana I., Bahama Is. where it is found, and which is also centrally located in relation to the other localities from which examined specimens derive.

Crassispira (*Monilispira*) *elatior* (C.B. Adams, 1845) (Figures 6–10)

Pleurotoma elatior C.B. Adams, 1845: 4: Krebs (1864: 9); Tryon (1884: 319); Clench and Turner (1950: 276, pl. 29, fig. 7); Robinson and Montoya (1987: 391).

Drillia elatior (C.B. Adams, 1845): Olsson and McGinty (1958: 18); Nowell-Usticke (1959: 81).

Crassispira adamsi de Jong and Coomans, 1988: 111 is an unnecessary replacement name. A homonym, *Pleurotoma elatior* d'Orbigny, was believed by these authors to have been published in 1842, but research by Rosenberg (2009) found 1847 to be the true publication date of the plate with name and drawing of this homonym [now = *Nanodiella elatior* (d'Orbigny, 1847)]. This replacement name has been used by Williams (2005, 2006, and 2009: number 3100) and Kirsh (2006: 17, fig. 21).

Crassispira elatior (C.B. Adams, 1845): García (2010: 12).

Description: Adams' original description was a small ornate shell, subconical, white, with an encircling dark band split by the suture. Spire elongate with 6 slightly convex whorls having 12 weak individual ribs; striae on shell base; anal sinus shallow; anterior canal short. Spire angle 22°, 3.2 mm; shell overall 4.8 × 1.9 mm.

Type Material: Holotype: MCZ 155923, a photograph of which appears in Clench and Turner (1950: pl. 29, fig. 7) and in Williams (2006 and 2009: number 3100, left photograph).

Type Locality: Jamaica.

Material Examined: 2 spec., 5.5 × 2.5 and 7.2 × 3.0 mm (Figures 6–8), from coral in shallow water, Pelican I., Barbados (USNM 502365); 1 spec., 6.9 × 2.8 mm (Figure 9), beach collected, Barbados (USNM 502364); 1 spec., 4.4 × 1.9 mm (Figure 10), E Colon I., Bocas del Toro, Panama, McGinty and Olsson! (ANSP 200027).

Distribution: SE Florida (Palm Beach Co.); Lesser Antilles (St. Martin; St. Croix; Barbados); and western Caribbean (Costa Rica; Panama).

Remarks: Adams did not describe the protoconch but his description of the teleoconch is consistent with photographs of the holotype and with the specimens examined for this project. De Jong and Coomans (1988: 111) report, for a 5.0 × 2.0 mm specimen from St. Martin, about 19 ribs on the penultimate. Adam's count must be a misprint because the holotype though worn appears in the photograph in Clench and Turner to have more than 12 ribs. Fresh specimens have a spirally ridged protoconch, not the dome-shaped, "ribbed" one reported by de Jong and Coomans (1988: 111). The protoconch whorls are low, smooth, with a single keel at the whorl summits (enlarged views of the protoconchs of specimens in Figures 6 and 7 are shown in Figure 8). De Jong and Coomans' St. Martin

specimen may have been worn, in which case the protoeoneh might appear dome shaped.

This is another of C.B. Adams' briefly deseribed and un-illustrated species. The first appearance of a photograph of the holotype was in Clench and Turner (1950). It showed the rather unique sculpture and color pattern, and not long after their publication investigators began reporting its occurrence from a wide area: Costa Riea (Robinson and Montoya, 1987); Panama (Olsson and McGinty, 1958); St. Martin (de Jong and Coomans, 1988); St. Croix (Nowell-Usticke, 1959); and Palm Beach Co., E Florida (Kirsh, 2006).

A ridged protoconch, or one with spirals, and a teleoeonch with beaded or retieulated surface are features shared by *C. nigreseens*, *C. latizonata*, *C. verbernei*, and *C. pellisphocae*. *Crassispira elatior* is easily reeognized by its uniformly small-beaded surface (appearing reticulated in worn speeimens), except in the sulcus where only the axial ribs show, and by its small size. *Crassispira elatior* can be further distinguished from *C. latizonata* by its lower, less exserted protoconch, smoother, rounder (not squarish) outline of the whorls, and rounder shell base. From *C. nigreseens* it can be distinguished by the absence of a smooth, heavy subsutural cord, and a smoother, rounder (not squarish) outline of the whorls. From *C. verbernei*, it ean be distinguished by a more slender profile and proportionally larger aperture, and from *C. pellisphocae* it differs in having a beaded surface, a peripheral white band, not uniformly brown or black, and a smaller size.

Crassispira (*Monilispira*) *nigreseens* (C.B. Adams, 1845) (Figures 11–15)

Pleurotoma nigrescens C.B. Adams, 1845: 3 [Jan.]: d'Orbigny (1847: 170); C.B. Adams (1850a: 54); Krebs (1864: 10); Dall (1885: 237); Paetel (1888); Clench and Turner (1950:315, pl. 29, fig. 11).

Not *Pleurotoma nigrescens* Reeve, 1845: pl. 26, no. 235 [Nov.], a junior homonym, = *Strictispira paxillus* (Reeve, 1845).

Drillia (*Crassispira*) *nigrescens* (C.B. Adams, 1845): H. and A. Adams (1853: 91); Tryon (1884: 173).

Crassispira nigrescens (C.B. Adams, 1845): Abbott (1958: 95); Nowell-Usticke (1959: 81); Work (1969: 679); Ekdale (1974: 650); Cubit and Williams (1983: 29); Maes (1983: 323); Kaicher (1984: eard 3984); D. Lamy et al. (1984); de Jong and Coomans (1988: 109); Leal (1991: 189, pl. 24, fig. F [of protoeonch only]); Espinosa et al. (1995: 43); Pointier and Lamy (1998: 59, text photo); Williams (2005, 2006, and 2009: number 3134); Fallon (2008: figs. 17a, b).

Crassispira (*Crassispirella*) *nigrescens* (C.B. Adams, 1845): Warmke and Abbott (1961: 135, pl. 25, fig. m); Powell (1966: 76); Abbott (1974: 273); Vokes and Vokes (1984: 30); Rios (1994: 167, pl. 55, fig. 760); Redfern (2001: 126, pl. 57, fig. 523A-C; pl. 112, fig. 523D). See under Remarks below about the possible misidentification of Abaco I. specimens.

Not Vokes and Vokes (1984: pl. 21, fig. 8 only): mislabeled photograph of *Agathotoma trilineata* as *C.* (*C.*) *nigrescens*; not Rios (1985: 141, pl. 48, fig. 653), which is *Agathotoma trilincata* (Tippett, pers. comm., 21 Apr 2009).

Crassispira (*Monilispira*) *nigrescens* (C.B. Adams, 1845): Rios (1983).

Ithycythara lanceolata anct. non (C.B. Adams, 1850): miscaptioning of *C.* (*C.*) *nigrescens* in Vokes and Vokes (1984: pl. 29, fig. 10).

Pyrgospira flavocincta anct. non (C.B. Adams, 1850): misidentifieation by Faber (2007: 124, figs. 30, 31) that may be this species.

Drillia ponciana Dall and Simpson, 1901: 386, pl. 57, fig. 19: a junior synonym according to Kaicher (1984: card 3984). The type locality is Playa de Ponce, Porto Rico; the holotype is in USNM 159684.

Drillia (*Clathrodrillia*) *ponciana* (Dall and Simpson, 1901): Abbott (1974: 270, fig. 3000).

Description: A speeimen from Limekiln Bay, Carriaeou I., Grenada, very close in appearance to the lectotype depicted by Clench and Turner (1950), has been selected for deseription here.

Shell 7.2 × 2.7 mm, of 8 slightly convex whorls, fusiform, anterior truncated; whorls patterned with heavy subsutural eord followed by rows of tightly packed beads (Figure 11). Protoconch pancispiral with ~2 whorls, smooth except last 0.5 whorl has 6 riblets; whorls not immersed, tip lies above level of second whorl. Teleoconeh with 6 whorls, first 2 with a single row of round beads, changing to 2, then to 3 by penultimate whorl. Beads are formed at interseetion of spiral and axial cords. Body whorl with 4 additional beaded rows, followed by 4–5 rows of slightly granulose to smooth cords that encircle siphonal eanal. Spiral threads, 0–3 in number, lie betweeu spiral cords. Subsutural cord, loeated near suture, sharply ridged. Sulcus narrow, about one-quarter width of spire whorls, concave, with reduced but thin lamellae-like curved rib extensions and growth striae, overridden by fine spiral threads. Ribs number 23 on penultimate, 19 on body whorl to varix. Varix eomprised of 3 swollen ribs. Aperture 31% of overall length of shell, narrowly oval ending anteriorly in a short, open, slightly notched siphonal canal. Outer lip thin but reinforced by two ribs; stromboid notch weak. Anal sinus deep, lies below sutural cord, and U-shaped, being partially closed at its entrance at edge of lip by parietal eallus and upward turn of outer lip. Inner lip thin, appressed along its length, ending in a parietal eallus that bridges space between parietal wall and upper side of anal sinus. Shell color brown, with spiral cords and siphonal canal paler; crests of beads and sutural cord lighter still.

Type Material: The lectotype (selected by Clench and Turner, 1950: pl. 29, fig. 11) is in MCZ 177354.

Type Locality: Jamaica.

Material Examined: 1 spec., 5.8 mm, at 2–3 m, in drifted sand on rocks, White Bay, Guana I., British Virgin Is., V.O. Maes!, 15–28 Feb 1975 (ANSP 338612); 1 spee. 6.9 × 2.8 mm at 4.6 m, Yomg I., SVG, G. Maekintosh!, 24 Jul 1998 (author's coll.); 1 spec. 6.6 × 2.7 mm, at 7.6 m, Petit Nevis, SVG, G. Maekintosh! 14 Jul 1996 (author's coll.); 14 spee., up to 7.8 × 3.0 mm (Figure 12), crabbed, intertidal, Clifton Harbor, Union I., SVG,

P. Fallon!, 16 Jun 2007 (author's coll.); 1 spec., at 0.9–1.5 m [3–5 ft] in weed, sand, some rock, 4.8 km [3 mi] NE of Ragged Pt., Barbados, R. and V.O. Maes! Dec 1963 (ANSP 291265); 3 spec., 5.9 × 2.3, 5.7 × 2.3, and 5.8 × 2.3 mm, at 6.7 m, S side of Molinere Pt., Grenada, G. Mackintosh! 18 Apr 2004 (USNM 1150456); 1 spec., 6.5 × 2.4 mm, at 7.3 m on silted reef, S side of Molinere Pt., Grenada, G. Mackintosh! 17 Jan 2007 (author's coll.); 1 spec., 6.5 × 2.5 mm, E side of Prickly Pt., SW Grenada, R. Ostheimer!, Jan–Feb 1964 (ANSP 296632); 6 spec. (4 very worn), N end of Grand Anse Beach, W Grenada (ANSP 297466); 2 spec., 7.2 × 2.7 (Figure 11) and 6.6 × 2.7 mm (broken apex), at 12.8 m, in rubble, Limekiln Bay, Carriacou I., Grenada, (USNM 1150457); 1 spec., 7.4 × 2.7 mm (Figure 13), harbor dredgings, Oranjestad, Aruba, Netherlands Antilles (ANSP 349135); 4 spec., best is 7.4 × 2.6 mm (Figure 14), Fernando de Noronha Is., Brazil, Jan 1979 (ANSP 350161); and 2 spec., 7.1 × 2.6 (Figure 15) and 7.6 × 2.7 mm, at 8–10 m on fine sand, San Blas Is., Panama (author's coll.).

Distribution: Greater Antilles: Cuba, Jamaica, Cayman Is., and Puerto Rico; Lesser Antilles: U. S. Virgin Is. to the Netherlands Antilles; Western Caribbean: Panama (San Blas Is.); and South America: Venezuela (Los Roques Is.), Trinidad and Tobago (Tobago I.), and Brazil (Fernando de Noronha Is., Pernambuco). Although not examined for confirmation (and no corresponding photographs were published in the sources) specimens have been reported from the Gulf of Mexico: Mexico (Vokes and Vokes, 1984: Arcas Cays, Campeche Bank); Western Caribbean: Mexico (Ekdale, 1974: between Cancun and Contoy Is.), and Panama (Cubit and Williams, 1983: Galeta Reef).

Remarks: *Crassispira nigrescens* is widely distributed and not uncommon, based on the number of publications in which it has appeared and localities reported. Although relatively well known, some confusion about its true identity persists. *Crassispira nigrescens* reported by Redfern (2001: 126, pl. 57, figs. 523A–C; pl. 112, fig. 523D) from Abaco I., Bahama Is., may be *C. mayaguanaensis*, a similar species but with distinctive differences (see comparison above under that species). No other published report of *C. nigrescens* from the Bahama Is. has been found. Some confusion in identity may be due to the geographic variability of the species. Although a fairly consistent pattern of surface sculpture occurs in specimens throughout its range (strong, sharply delineated subsutural cord, narrow sulcus, 3 beaded spiral cords), noticeable differences in the relative size of various elements of this pattern are evident among geographically separate populations. Geographic variability is not unexpected given the species' apparent confinement to island habitats and its attendant isolation into small populations. Photographs of similarly-sized specimens from several different localities are shown in Figures 11–15. The relative size of the beads and number of beaded cords on the spire whorls are variable characters, as is color. The extremes in bead size are exhibited by the Grenadian specimen with the largest (Figure 11), and the Fernando de Noronha Is. specimen with the smallest beads (Figure 14). This latter specimen also has finer cords and more rows of beaded cords on the spire whorls than the typical form. It may eventually prove to be a separate species when a sufficient number of specimens has been examined. Color also appears to vary with populations, though the small sample size precludes any general statement about specific populations. Specimens examined from Aruba and Fernando de Noronha Is. shown in Figures 13 and 14 are lighter colored than the ones shown from other localities.

Crassispira (*Monilispira*) *latizonata* (E.A. Smith, 1882) (Figures 16–20)

Pleurotoma (*Crassispira*) *latizonata* E.A. Smith, 1882: 212–213.

Crassispira latizonata (E.A. Smith, 1882): Rios and Barcellos (1979: 164); Leal (1991: 188–189, pl. 24, fig. E); Williams (2005: number 3105, left photograph only); Barros et al. (2005: 147, fig. c); Williams (2006 and 2009: number 3105, left photographs only).

Crassispira (*Crassispirella*) *latizonata* (E.A. Smith, 1882): Rios (1985: 141, pl. 48, fig. 652); Rios (1994: 167, pl. 55, fig. 759); Kantor et al. (1997: 56, 61–62, fig. 7 [subgenus with question mark on p. 56, but not on p. 61]); Rios (2009: 324, fig. 828).

Drillia ponciana var. *virgata* Usticke, 1969. Nowell-Usticke, 1969: 27, pl. 5, fig. 1098: a synonym according to Rosenberg (2009). The type locality is Barbados; the lectotype is in AMNH 195457 (designated as "holotype" by Nowell-Usticke, 1971: 22, but corrected to lectotype by Boyko and Cordeiro, 2001: 60).

Drillia bandata Usticke, 1971: 22, pl. 4, fig. 1088: is not *Crassispira bandata* (Usticke 1969). *D. bandata* was an unnecessary replacement name for *Drillia virgata* (Usticke, 1969), as Nowell-Usticke incorrectly assumed his *Drillia ponciana* var. *virgata* was preoccupied (see Faber, 1988: 72). Nowell-Usticke intended to elevate the taxon to species-group level.

Description: The specimen described here, from Falmouth Bay, Antigua, matches Smith's description of the type shown in Figure 16, allowing for differences exhibited by a less mature shell (Figure 17). The holotype is believed to be an exceptionally large specimen (8.9 × 3.5 mm). The type of *Drillia virgata* (from Barbados) is comparably sized at 8.5 mm in length.

Shell narrowly fusiform with truncated anterior, 6.3 × 2.4 mm, of 6.75 slightly convex whorls, aperture 36% of overall shell height (holotype with 8+ whorls). Surface covered, except in a narrow sulcus, with closely-packed rows of beads (Figure 17). Protoconch with 1.75 whorls, first 1.25 smooth, with cord on summit creating square shoulder (Figure 18). Protoconch identical to that figured for Brazilian *C. latizonata* by Leal (1991: pl. 24, fig. E). (Although worn, cord still visible on holotype.) Cord absent on last 0.5 turn but instead there are ~10 angled riblets, forming a slight shoulder below summit of whorl. Teleoconch begins with abrupt appearance of a spiral cord mid-whorl, with narrow axials angled at intersection of mid-whorl cord, beaded at angle, and

with appearance of a subsutural cord, here beaded, not smooth. A third spiral cord appears below central one on third whorl, and a fourth on fourth whorl. Five, including subsutural cord, are on penultimate whorl. Body whorl with 11 spiral cords: 5 above suture line followed by 3 beaded cords on shell base and 3 granulose cords on siphonal canal. Body whorl with 18 axials, last 3 forming a varix, and 19 on penultimate whorl. Sulcus narrow, with a few faint spiral threads visible on last whorl that undulate over ribs and with fine incremental growth lines of same open curvature as sinus. Ribs present but reduced in sulcus. Subsutural cord slightly thinner than peripheral cords, and lies at or just below suture. Outer lip plain, without a stromboid notch. A shallow notch present in holotype. Anal sinus anterior to sutural cord, shallow and broad, possibly because of immature condition of examined specimen. Holotype, a mature shell, witha U-shaped sinus constricted at opening above by parietal callus. Inner lip appressed to columella and parietal wall, a very slight lobe at juncture of outer lip, not the heavy tubercle in type specimen. Anterior canal is very short. Shell color a light golden brown with a band consisting of 3 rows of white spiral beads on shell's periphery, and another with 2 rows of white beads on shell's base, below suture line. Apex also white.

Type Material: Holotype: NHMUK 1874.5.26.88.

Type Locality: Unknown to E.A. Smith.

Material Examined: Holotype, 8.9 × 3.5 mm (Figure 16), no locality; 2 spec., 6.3 × 2.4 (Figures 17–18) and 6.4 × 2.5 mm (Figure 19), from under rocks at 2–3 m, Falmouth Bay, Antigua, M. Coltro! (USNM 1150458); 4 spec., 5.4, 6.5 (Figure 20), 6.8 and 6.8 mm, Fernando de Noronha Is., Brazil (ANSP 350160).

Distribution: Lesser Antilles (Antigua, Barbados) and Brazil (Fernando de Noronha Is.), in intertidal to 3 m depths (as reported for the Antigua and Brazil localities).

Remarks: Smith's taxon was published without illustration and without locality; it remained largely unknown for almost a century. Specimens from Fernando de Noronha Island were first recognized by Brazilian workers as *C. latizonata* (Rios and Barcellos, 1979; Rios 1985; Leal, 1991; Rios 1994). Somewhat earlier, in his 1969 publication, and probably unaware that this species had already been described, Nowell-Usticke published a new description of a specimen from Barbados, naming it *Drillia ponciana* var. *virgata* Usticke, 1969. He described it as having 1.5 swirled nuclear whorls, 7 whorls with packed rows of white beads, without a strong subsutural cord, and a brown sutural band. He further noted that the shell base has brown beading, which turns into brown spiral cords. Like the type of *C. latizonata*, his specimen from Barbados is quite mature, 8.5 × 3.2 mm (see Williams, 2006: number 3105, second photograph from the left). In his 1971 publication, Nowell-Usticke emended his description to include "1 ½ swirled, **keeled** nuclear whorls" (emphasis added). The keeled protoconch (and less prominent sutural cord) clearly distinguishes this species from *C. nigrescens* and from *C. mayaguanaensis*, which have smooth protoconchs. A photograph of the protoconch of *C. latizonata* appears in Leal (1991: pl. 24, fig. E), and is described as "paucispiral, with 1¼ whorl and has a squarish profile to its shoulder."

Rios (1985: 141) described this species as 6 × 2 mm, 6 whorls, pale-yellow with light-brown spiral bands, and with a sculpture of "beaded spiral rows (22 to 23 beads on the two last whorls). Base with 6 to 7 spiral threads." It is not clear from Rios' description how many beaded cords are present on the shell base, but the photograph provided in pl. 42, figure 652, appears to be this species, smaller and narrower than the type, but like the specimen described herein.

Crassispira (*Monilispira*) *verbernei* de Jong and Coomans, 1988
(Figures 21–23)

Crassispira verbernei de Jong and Coomans (1988: 111, pl. 17, figs. 589A, B; pl. 43, fig. 589); Williams (2005, 2006, and 2009: number 3108).

Monilispira verbernei (de Jong and Coomans, 1988): Faber (2007: 124).

Description: According to de Jong and Coomans, holotype is 4.8 × 2.2 mm, of 6 whorls with 1 nuclear whorl; shell moderately convex. Protoconch shows 3 weak spirals. Outer lip sharp, thickened behind, continued around top of aperture as a thick callous pad. Colour greyish- or orange-brown, with a broad white (anal) band below suture; lower half of base also white. Lower halves of whorls with dark brown lines (6 on body whorl), coinciding with spiral grooves. An all-brown color form exists, a few of which are paler below suture.

Type Material: Holotype: ZMA 3.87.097; several paratypes are in ZMA 3.87.169 and ZMA 3.87.170 (Williams, 2005: number 3108). A photograph of the holotype is in de Jong and Coomans (1988: pl. 43, fig. 589).

Type Locality: Aruba, west coast.

Material Examined: 1 spec., 4.8 × 2.1 mm (Figure 21), harbor dredgings, Oranjestad, Aruba, Netherlands Antilles, Frère Fredericus! (ANSP 349132); 1 spec., 4.7 × 2.1 mm (Figure 22), harbor dredgings, Oranjestad, Aruba, Frère Fredericus! (ANSP 349133); 1 spec., 5.1 × 2.1 mm (Figure 23), at 7.6 m, La Blanquilla I., Venezuela, G. Mackintosh!, 4 Jan 2000 (USNM 1150459); 1 spec., 4.6 × 2.1 mm (protoconch missing), Aruba, locality not specified, M. Beerman! (author's coll.).

Distribution: The only published occurrence is on Aruba's west coast. A specimen in USNM 902239 from Los Roques, Venezuela, (5.4 × 2.2 mm, under rocks at

3 ft [0.9 m], G. Duffy!, 24 Mar 1996) is this species (Tippett, pers. comm., 19 Aug 2009). This specimen and the one from La Blanquilla I. indicate that this species is not endemic to Aruba but also occurs near other islands off Venezuela. A specimen in the Florida Museum of Natural History (FLMNH 231607) from Bocas del Toro Prov., Panama (L. McGinty!, 1951) catalogued as this species needs to be confirmed.

Remarks: The typical color pattern described by de Jong and Coomans, brown with a broad white band below the suture, is shown in Figure 21. An all-brown color form shown in Figure 22 agrees well with their description, but the protoconch is worn smooth so its 3 weak spirals are absent. Other color forms are depicted in Williams (2006: number 3108, paratypes in ZMA 3.87.170). There are 3 other species in *Monilispira* with spiral cords present on the protoconch but the form of the protoconch is quite different for each: *C. elatior*, *C. latizonata*, and *C. pellisphocae*. The protoconchs of *C. pellisphocae* and *C. verbernei* are depicted in SEMs by de Jong and Coomans (1988: pl. 17, figs. 588 and 589A). Protoconchs of *C. elatior*, *C. latizonata*, and *C. pellisphocae* are illustrated in Figures 8, 18 and 27, respectively. *C. elatior* has a single keel, *C. verbernei* 3 fine spirals, *C. pellisphocae* a keel and basal cord, and *C. latizonata* a single keel, with the protoconch more "telescoped" than that of *C. elatior*. There are other differences too. *Crassispira verbernei* is most similar to *C. pellisphocae*, which is about twice its height (to 8.5 mm according to de Jong and Coomans, but up to 11 mm for specimens from St. Croix according to Nowell-Usticke, 1959: 81), and has cancellation overall except in the sulcus versus limited to the base in *C. verbenei*.

A specimen from La Blanquilla I. (Figure 23) may be indicative of regional variation. It has a more streamlined profile, a narrower sulcus, and a more pinched anterior. More material needs to be examined to asses whether this population has consistent differences from that on Aruba.

Crassispira (*Monilispira*) *pellisphocae* (Reeve, 1845) (Figures 24–28)

Pleurotoma pellis-phocae Reeve, 1845: pl. 29, fig. 263; Dall (1885: 238).

Pleurotoma pellisphocae Reeve, 1845: Paetel (1888).

Defrancia pellisphocae (Reeve, 1845): H. and A. Adams (1853: 96); Paetel (1888).

Lachesis pellisphocae (Reeve, 1845): Tryon (1884: 225, pl. 27, fig. 3).

Crassispira pellisphocae (Reeve, 1845): de Jong and Coomans (1988: 110, pl. 17, figs. 588A, B; pl. 43, fig. 588); Williams (2005, 2006, and 2009: number 3133); Fallon (2008: 12, 13, figs. 19a, b, erroneously captioned as *Strictispira pellisphocae*).

Crassispira (*Monilispira*) *pellisphocae* (Reeve, 1845): Maes (1983: 322, figs. 16, 25, 32).

Monilispira pellisphocae (Reeve, 1845): Faber (2007: 124, figs. 27–29).

Pleurotoma cancellata Reeve, 1846, *non* Eichwald, 1833: Synonymized here by Tomlin (1934: 40). St. Vincents [sic], W. Indies is written on the original mounting board and so is taken as the type locality. Two syntypes are in NHMUK 1875.4.26.17. These were verified as *C. pellisphocae* for this work.

Chauvetia pellis-phocae (Reeve, 1846): erroneous reassignment to a buccinid genus by Tomlin (1934: 39).

Drillia cancellata (Reeve, 1846): Nowell-Usticke (1959: 81).

Clathrodrillia limans Dall, 1919: 14, pl. 13, fig. 3: a junior synonym according to Maes (1983: 322). The type locality is "Gulf of California", which is in error according to McLean (1971b: 907). The holotype is in USNM 56218.

Crassispira? Gibson-Smith, 1972: 475 is this species according to Maes (1983: 322).

Description: Reeve's type is a worn specimen (Figure 24), so a 7.5 × 3.1 mm specimen from Union I., SVG is described (Figure 25).

Shell fusiform, truncated on anterior end, 8 slightly convex whorls; aperture about 41% of shell height. Shells attain at least 10.8 mm in height. Protoconch is worn smooth, but in a young specimen has ~1.5 whorls bearing 2 spiral cords, 1 at crest of whorl, other at bottom, next to suture with succeeding whorl; last 0.25 whorl with riblets in addition to the 2 cords (Figure 27). Upper cord gives protoconch a ridged, flat-top appearance, but sloped, as nuclear whorl rises from center axis of protoconch. Both cords move to center of post-nuclear whorls, subsutural cord arising above them on first teleoconch whorl. Teleoconch with ~6 convex whorls with peripheries slightly below midwhorl. Axial and spiral cords subequal, evenly spaced, giving surface reticulated appearance. Spirals override axials, and are lighter in color. Subsutural cord of same size as spirals, in narrow sulcus a little wider than space between succeeding spiral cords; close-packed threads between each of spiral cords and in sulcus. In some specimens, sulcus is wider (Figure 28). Sulcus has traces of axials, which are hooked to left, marked with heavy arcuate growth striae. On body whorl, axials evanesce on shell base where spiral cords then become dominant. Up to 4 spiral cords on spire whorls, exclusive of subsutural cord (early whorls have fewer), and 5 more on shell base, where tiny beads form at the intersection of radial cords in some. Additionally, 5 cords encircle siphonal canal. Axials ~22 on body whorl to varix, 30 on penultimate whorl. Varix a low, broad swelling behind anal sinus. Outer lip thin, without stromboid notch. Anal sinus deep and U-shaped, bordered by parietal callus, and acutely angled toward shell axis, without an appreciable constriction of opening. Two small ribs present near edge of outer lip. Inner lip thin, appressed to parietal wall. Aperture narrow, ending in short, open siphonal canal.

Type: Holotype: NHMUK 1879.2.26.43, a single specimen lot (identified as the holotype by Maes, 1983: 322). It is illustrated in Faber (2007: 124, fig. 27, captioned "syntype 1"). In the same paper, Faber's figures 28

and 29 (syntypes in NHMUK 1875.4.26.17) are the types of *P. cancellata* Reeve, 1846, a junior synonym.

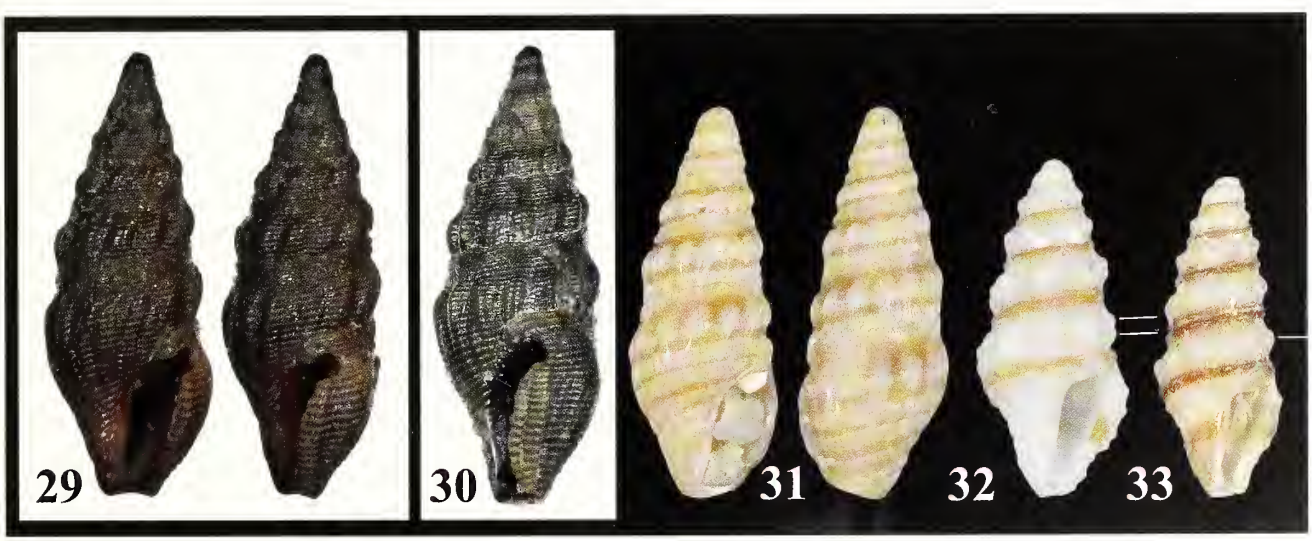
Type Locality: Unknown to Reeve. It is here designated as Union I., St. Vincent and the Grenadines.

Material Examined: Type in NHMUK 1879.2.26.43, 9.2 × 3.7 mm, type locality not stated; 1 spec., at 8–10 ft [2.4–3.0 m], off Fowey Rock, Miami-Dade Co., E Florida (USNM 902234); 1 spec., 8.1 x 3.5 mm, on coral rubble at 0.3–0.9 m [1–3 ft], Media la Luna, off La Parguera, Puerto Rico, T. Watters!, 27 Apr 2009 (T. Watters coll.); 10 spec., 7.4 × 3.0, 7.8 × 2.9, 7.5 × 2.9, 8.4 × 3.2, 7.8 × 3.0, 7.7 × 3.0, 7.5 × 2.8, 7.3 × 2.6, 6.5 × 2.5, and 5.7 × 2.5 mm, at 4.6 m on large rocks at night, Young I., SVG, G. Mackintosh! 24 Jul 1998 (author's coll.); 306 spec., up to 9.9 × 3.9 mm (Figures 25, 26, 27), crabbed, intertidal, Clifton Harbor, Union I., SVG (author's coll.); 5 spec., 6.9 × 2.7, 6.8 × 2.7, 6.4 × 2.3, 6.6 × 2.5 and 7.0 × 2.7 mm, at 6.7 m, S side of Molinere Pt., Grenada, G. Mackintosh! 18 Apr 2004 (author's coll.); 25 spec., to 7.4 × 2.9 mm, 7.3 m, S side of Molincre Pt., Grenada, G. Mackintosh! 17 Jan 2007 (author's coll.); 1 spec., 6.8 × 2.7 mm, on coral sand/rubble, Carriacou I., Grenada, T. McCleery! May 2004 (author's coll.); 1 spec., 8.5 × 3.2 mm, at 6.1 m, Ronde I., Grenada, G. Mackintosh!, 6 Jun 1998 (author's coll.); 3 spec., 8.2 × 3.0, 7.2 × 2.8, and 7.4 × 2.7 mm, at 11 m, Man of War Bay, Tobago I., Trinidad and Tobago, G. Mackintosh!, 6 Jun 1998 (author's coll.); 1 spec., 10.7 × 4.2 mm, Malmok, Aruba, in 2–9 m, A. Bodart and L. Couto!, Nov 1996 (USNM 902237); 5 spec., 10.8 × 4.3 (Figure 28), 10.8 × 4.0, 10.6 × 4.1, 10.1 × 4.2, and 9.0 × 3.3 mm, at 4–10 m, Cabo de La Vela, Colombia, A. Jorio and L. Couto! (author's coll.).

Distribution: Florida: E Florida (Miami-Dade Co.); Bahama Is., (Eleuthera I.); Greater Antilles: Dominican Republic, Puerto Rico; Lesser Antilles: U. S. Virgin Is. (St. Thomas, St. Croix), Br. Virgin Is. (Guana I., Antigua I., Barbuda I.), SVG (St. Vincent I., Union I.), Grenada (Grenada I. Calivigny I., Carriacou I., Ronde I.), Netherlands Antilles (Curaçao, Aruba, Bonaire); and South America: Trinidad and Tobago (Tobago I.), Colombia, and Venezuela (Falcon: offshore Is.).

Remarks: Only incomplete descriptions have been published in the literature (Reeve, 1845: pl. 29, fig. 263; Maes, 1983: 322, figs. 16, 25, 32; and de Jong and Coomans, 1988: pls. 17, 43, figs. 588A, B). Photographs are of generally poor quality because *C. pellisphoeae* is uniformly black, resulting in poor definition of the fine detail of the shell's sculpture. The distinctive protoconch is nicely illustrated by Maes (1983: fig. 25), and also by de Jong and Coomans (1988: pl. 17, fig. 588). The whole shell illustrated by Maes (1983: fig. 16) is subadult, and the structure of the mature lip is lacking.

This species is distinctive with its axials and spirals nearly the same size, and equally spaced giving it a fine, cancellate appearance. The closest species is *C. verbernei*, de Jong and Coomans, 1988, which is smaller, nodulous, not cancellate, and usually more colorful, not the uniform black or dark brown of *C. pellisphoeae*. It differs from *C. nigreseens* in being broader, in lacking the beaded spirals, in having a finer subsutural cord, and in having a ridged protoconch.



Figures 29–33. *Crassispira* species. **29–30.** *Crassispira* (*Monilispira*) *guildingii* (Reeve, 1845). **29.** Lectotype in NHMUK 1875.4.26.18, St. Vincent, 8.3 × 3.3 mm. **30.** USNM 1150460, Young I., SVG, 8.5 × 3.5 mm. **Figure 31.** *Crassispira* (*Dallspira*) *flavocincta* (C.B. Adams, 1850), ANSP 371999, Port Royal, Jamaica, 5.1 × 2.1 mm. Dorsal and ventral views. **Figures 32–33.** *Crassispira* (*Dallspira*) *bandata* (Usticke, 1969). **32.** ANSP 298618, off E coast, N end Elbow (Little Guana) Cay, Great Abaco, Bahama Is., 4.4 × 1.9 mm. The two rows of nodules on the penultimate whorl are indicated by lines. **33.** ANSP 291177, 1 mi N of Holetown, Barbados, 4.2 × 1.7 mm. This specimen has only a single row of large peripheral nodules.

Crassispira (*Monilispira*) *guildingii* (Reeve, 1845)
(Figures 29–30)

Pleurotoma guildingii Reeve, 1845: pl. 30, fig. 268: Reeve (1846: 116); d'Orbigny (1847: 170, no. 365); Gray (1854: 30, number 365); Beau (1858: 7); Krebs (1864: 9); Arango y Molina (1878: 219); Dall (1885: 236); Paetel (1888).
Defrancia guildingii (Reeve, 1845): H. and A. Adams (1853: 96); Paetel (1888).
Clathurella guildingii (Reeve, 1845): Gould (1862); Tryon (1884: 279, pl. 18, fig. 44).
Crassispira guildingii (Reeve, 1845): Williams (2005, 2006, and 2009: number 3132).

Description: The specimen described here is almost identical to the best of Reeve's 3 lectotypes, and depicted in Figure 29.

Shell with 8 convex whorls, is 8.5 × 3.5 mm, biconic, truncated anteriorly, and aperture, including canal about 44% of total height of shell (Figure 30). Protoconch 2 smooth whorls, black in color, ending where incised spiral lines begin, marking beginning of adult sculpture. No riblets visible on protoconch, possibly because of its slightly worn condition. Teleoconch whorls all about the same, with wide, flat sulcus about a third of height of spire whorls. Suture appressed and undulating over the ribs. Below, round, broad ribs run to the succeeding suture, numbering 11 to varix, 13 on penultimate; on body whorl they evanesce on shell base. A few narrower, shorter ribs present adjoining larger ribs on body whorl. Varix a swollen rib, ~0.25 turn behind outer lip. Entire surface of teleoconch covered with fine spiral cords, most separated by 1–2 fine threads; cords slightly larger on ribs shoulder and in sulcus posterior-most 2–3, just below the suture, which form subsutural fold. Spiral cords a dirty, slightly translucent white; threads black, giving shell a dusky color. Outer lip thin but reinforced by 2 small ribs behind, in front of varix; no stromboid notch. Inner lip thin and narrow, appressed to columella and parietal wall. Parietal callus present at junction of inner and outer lips. Anal sinus deep and u-shaped, positioned between subsutural fold and callus, and shoulder formed by ribs, its opening slightly constricted by parietal callus. Anterior canal short, open and not otherwise distinguished from aperture, covered with ~10 spiral cords that are the same as on shell proper.

Type Material: Three syntypes: NHMUK 1875.4.26.18. The one in better condition, as suggested by Tippett (pers. comm., 19 Aug 2009), is here designated the lectotype. The two paralectotypes are in poor condition and not illustrated.

Type Locality: St. Vincent, West Indies.

Material Examined: Lectotype in NHMUK 1875.4.26.18, 8.3 × 3.3 mm (Figure 29), and 2 paralectotypes also in NHMUK 1875.4.26.18, 9.3 × 3.7 and 8.1 × 3.3 mm; 1 spec., 8.5 × 3.5 mm (Figure 30), in 4.6 m, Young I., SVG, G. Mackintosh!, 3 Sep 2000 (USNM 1150460).

Distribution: Reported in mid-nineteenth Century literature from Cuba (d'Orbigny, 1847, Gray, 1854, and Arango y Molina, 1878), Guadeloupe (Beau, 1858 and Krebs, 1864), and "St. Vincent". The only recent reports are from St. Vincent I. (Williams, 2005, 2006, and 2009; Coltro and Coltro, 1999: Photo Gallery).

Remarks: This taxon was first combined in *Crassispira* in an early version of the online database Malacolog (Rosenberg, 2009), and followed by Williams (2005) in publication. Its unique sculpture of broad ribs, a wide flat sulcus, and the lack of spirally beaded cords, set it apart from the rest of the *Crassiclava*.

This species has not been reported in the literature for over 120 years. Photographs of the specimen in Williams (2005: number 3132) and on the Femorale, Inc. web site (Coltro and Coltro, 1999) from St. Vincent appear to be this species. Its scarcity in published reports is likely explained by its very limited natural range, as well as by its inconspicuous black color and small size (8–9 mm). The occurrence of this species in Cuba, as reported by d'Orbigny, might be verifiable since the inventory of his specimens in the British Museum is listed in Gray (1854) and thus available for verification.

Subgenus *Dallspira* Bartsch, 1950

Type Species: *Dallspira dalli* Bartsch, 1950, by original designation.

Remarks: This is a small, obscure group of rare crassispirines about which little is known. The genus was erected to accommodate two eastern Pacific species that may have little in common with the western Atlantic species other than some similar sculptural elements. According to Bartsch (1950: 92–93): shell with 2 smooth protoconch whorls, and a third of small axial riblets; sulcus moderately broad and moderately concave; subsutural cord feeble or lacking altogether; anal sinus deep and round, partially constricted, and adjoining a thick parietal knob; varix thickened, lying a short distance from the edge of the outer lip, edge protracted, sinuous; axial ribs or just nodules present, and nodulous spiral cords on the base of the shell; anterior canal short, broad; and inner lip reflected over and appressed to columella.

Western Atlantic species are typically much smaller (4–7 mm) than the eastern Pacific species (14–17 mm). Characteristics of both groups of species, which also set this subgenus apart from the others in *Crassispira*, are the presence of nodulous ribs or just nodules, and nodulous spiral cords on the base of the shell. Unlike the eastern Pacific species, the three TNWA species discussed here have a distinctive spiral cord. More work is necessary to determine whether a close phylogenetic relationship between the eastern Pacific and TNWA species to justify their grouping.

Crassispira (Dallspira) flavocincta (C.B. Adams, 1850)
(Figure 31)

Pleurotoma flavocincta C.B. Adams, 1850b: 63–64: Clench and Turner (1950: 281, pl. 29, fig. 1); Olsson and McGinty (1958: 18).
Crassispira flavocincta (C.B. Adams, 1850): de Jong and Coomans (1988: 110); Williams (2005, 2006, and 2009: number 3102).
Not *Pyrgospira flavocincta* (C.B. Adams, 1850): Faber (2007: 124, figs. 30, 31) =? *Crassispira nigrescens* (C.B. Adams, 1845).

Description: According to Adams (1850b: 63–64): shell ~4.8 × 1.8 mm, elongated, ovate-conic, ~7 nearly rectilinear whorls, slightly convex, with an indistinct suture. Protoconch moderately pointed. Whorls with a row of nodules around the middle, a subsutural cord above, and a third cord of intermediate size below. (Adams does not refer to the mid-whorl sculptural elements as nodules, but rather as a "very broad moderately elevated spiral ridge" that is "plicately and transversely ribbed", which has been interpreted here as simply "nodules".) Color white, with spiral bands of yellowish brown above and below the cords, and yellowish brown in between the nodules. Aperture small, wide, anal sinus near the upper end of the outer lip, anterior canal very short.

Type Material: Holotype: MCZ 155917. A photograph of the holotype is in Clench and Turner (1950: pl. 29, fig. 1), and also in Williams (2006 and 2009: number 3102).

Type Locality: Jamaica.

Material Examined: 1 spec., 5.1 × 2.1 mm (Figure 31), Port Royal, Jamaica (ANSP 371999).

Distribution: The only confirmed specimens are from Jamaica; unconfirmed reports of this species are from Panama (E. Colon I.), and the Netherlands Antilles (Curaçao, Aruba).

Remarks: No fresh specimens have been examined to add to Adams' description. The holotype is beach worn judging from its appearance in the photograph in Clench and Turner (1950: pl. 29, fig. 1), and as a consequence there is still some uncertainty about its true identity and the validity of specimens identified as this by some. The identification of specimens reported by Olsson and McGinty (1958) and de Jong and Coomans (1988) has not been confirmed. The specimen in ANSP 371999 is slightly larger than the type (5.1 versus 4.8 mm), but agrees well with Adams' description, and Clench and Turner's photograph, so is illustrated here in Figure 31, but it too, is a worn, polished shell.

Two shells from Aruba illustrated in Faber (2007: figs. 30, 31) are labeled as this species but are more likely *C. nigrescens* (C.B. Adams, 1845). They closely resemble the specimen of *C. nigrescens* from Aruba depicted in Figure 13. The approximately 8.4 and 10.0 mm heights given for specimens in Faber's figs. 30 and 31 are much larger than the 5.1 mm for confirmed specimens of *C. flavocincta*. (The length of an unconfirmed specimen is given as 6.6 mm by de Jong and Coomans, 1988.) *Crassispira nigrescens* has been reported to reach 8.5 mm (Nowell-Usticke, 1959, for *Drillia ponciana*, a junior synonym). Faber attributes placement in *Pyrgospira* to Maes (1983), which could not be verified. Photographs of *C. flavocincta* do not show the pinched body whorl characteristic of *Pyrgospira*.

After about 108 years of anonymity, *C. flavocincta* was "rediscovered" by Olsson and McGinty (1958) and reported in their Panamanian samples, and then again 30 years later by de Jong and Coomans (1988) in samples from the Netherlands Antilles. The use of this taxon may have been precipitated by the publication of photographs of Adams' types by Clench and Turner in 1950 as no reports of this species could be found in the literature before that time. Adams' descriptions were preliminary, and on account of his untimely passing at age 39 they were never followed by the more complete monograph he had intended (Clench and Turner, 1950: 234). As a consequence, many of his names went unused until after the appearance of Clench and Turner's publication.

Crassispira (Dallspira) fuscocincta (C.B. Adams, 1850)
(Not figured)

Pleurotoma fuscocincta C.B. Adams, 1850b: 62: Krebs (1864: 9); Tryon (1884: 319); Dall (1885: 235–236); Clench and Turner (1950: 285, pl. 30, fig. 6).
Cerodrillia fuscocincta (C.B. Adams, 1850): de Jong and Coomans (1988: 112).
Crassispira fuscocincta (C.B. Adams, 1850): Williams (2005, 2006, and 2009: number 3103, photograph of type only).

Description: According to Adams (1850b) for a shell measuring 6.9 × 3.3 mm: "Shell clavate pyramidal: pale yellowish white, with a sutural line of brown, anteriorly wax yellow with revolving lines of yellowish white: with a spiral series of large smooth well rounded nodules, on slightly elevated wide ridges on the lower half of the whorls; anteriorly with a few spiral raised lines: apex acute: spire with the outlines rectilinear: whorls seven or eight, not convex, with the suture not impressed: aperture rather wide: canal very short." Note that Adams uses the term nodules in this instance, but not in the description of *C. flavocincta*, where they are smaller, not so obviously round, more numerous, and thus presumably not meeting Adams' definition thereof.

Type Material: Holotype: MCZ 155958, a photograph of which is in Clench and Turner (1950: pl. 30, fig. 6).

Type Locality: Jamaica.

Distribution: Other than the type specimen collected by Adams in Jamaica, it has only been reported from Curaçao, Netherlands Antilles, by de Jong and Coomans (1988: 112).

Remarks: Little is known about this species because the type is a much-worn specimen. Its placement in *Dallspira* is based on Adams' description. No confirmed representative of this taxon, other than the single worn type, is available to expand its description. The name had not been used for over 140 years before de Jong and Coomans (1988: 112) applied it to an un-figured specimen from Curaçao. Attempts to locate these authors' specimen have so far been unsuccessful. The holotype appears similar to, and it has been suggested (Williams, 2006) that *Crassispira bandata* (Usticke, 1969) might be the same. *C. bandata* is a fairly distinctive species; photographs of a fresh specimens have been published (Redfern 2001; Williams, 2005), there is little doubt as to the identity of this taxon, discussed next in this work. The two species have some striking similarities: a white shell with a contrasting brown subsutural cord and a row of large rounded mid-whorl nodules (as best that can be made out in the photograph of the worn holotype of *C. fuscocincta*). The disparity in Adams' *C. fuscocincta* and Nowell-Usticke's *C. bandata* is one of size. The latter has been reported to be a maximum of 4.5 mm, while the former holotype is 6.9 mm. De Jong and Coomans gave the size of the only other reported specimen as 10.5 mm. These size differences make it unlikely that all three are the same species. A full understanding of this taxon will remain in doubt until specimens matching the type can be found.

Crassispira (*Dallspira*) *bandata* (Usticke, 1969)
(Figures 32–33)

Psarostola bandata Usticke, 1969: 17, pl. 3, fig. 766.
Monilispira bandata (Usticke, 1969): new combination used by Nowell-Usticke (1971: 22).
Crassispira bandata (Nowell-Usticke [sic], 1969): Redfern (2001: 126, pl. 57, fig. 524). Note that Nowell-Usticke used only "Usticke" in species authorship; but he used "Nowell-Usticke" in the authorship of his publications.
Crassispira bandata (Usticke, 1969): Williams (2005, 2006, and 2009: number 3101, right photograph only).

Description: Nowell-Usticke (1971: 22–23) described the holotype as having 6.5 rough and knobby whorls with slightly pointed nodules, and 1.5 smooth rounded protoconch whorls. The early whorls of the teleoconch have 1 and later ones 2 rows of nodules below the subsutural cord. The otherwise creamy white shell is set off by a thin shiny orange-brown sutural band, which includes the subsutural cord, and another close to the anterior end of the shell, visible on the body whorl. The narrow base of the shell has 4 granular spiral cords and ends in a short canal. The outer lip has a small anal sinus, and a varical hump behind. One of the 2 ANSP specimens (ANSP 298618, Figure 32) has 6 ribs to the varix on the body whorl, which are formed by the longitudinal alignment of the knobs; the penultimate has 8. The outer lip is thin and has a stromboid notch. The inner lip has a small callus at the junction of the inner and outer lips. The anal sinus is deep and open, and acutely angled to the shell's axis.

Type Material: Holotype: AMNH 195459 and measures 4.25 × 2.1 mm. According to Boyko and Cordeiro (2001: 105), it is a single specimen lot. A photograph of the holotype is in Nowell-Usticke (1969: pl. 3, fig. 766, and 1971: pl. 4, fig. 1103).

Type Locality: Christiansted Harbor, St. Croix.

Material Examined: 2 spec., 4.4 × 1.9 (Figure 32) and 4.3 × 1.8 mm (much worn), off E coast, N end Elbow (Little Guana) Cay, Great Abaco, Bahama Islands, Robert Robertson! (ANSP 298618); 1 spec., 4.2 × 1.7 mm (Figure 33) in 3–20 ft [0.9–6.1 m] on reef, 1 mi [1.6 km] N of Holetown, Barbados, R. and V.O. Maes! Dec 1963 (ANSP 291177); 1 spec., 3.9 × 1.7 mm, beach-collected, Loblolly Bay, Anegada I., British Virgin Islands, A. J. and J. C. Ostheimer! 13 Mar 1960 (ANSP 249486).

Distribution: Bahama Islands: Abaco Is.; and Lesser Antilles: U. S. Virgin Is. (St. Croix), Br. Virgin Is. (Anegada I.), and Barbados.

Remarks: This species is quite unmistakable because of its small size (~4 mm), white with brown sutural band, and knobby sculpture. There is no other species that resemble it except *C. fuscocincta* (see above). Its small size probably accounts for its scarcity in collections.

The sculpture varies among specimens examined. A single row of beading (instead of two), is seen in one of the ANSP specimens; the beads become vertically elongate on the body whorl, appearing like the two rows have not been split by an incised line (Figure 33). The orange-brown sutural band varies in width, as can be seen in the photographs of two ANSP specimens (Figures 24, 25). The band is almost entirely confined to the subsutural cord on the holotype, as is most clearly seen in the photograph in Williams (2005: number 3101).

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New fossil *Bathymodiolus* (sensu lato) (Bivalvia: Mytilidae) from Oligocene seep-carbonates in eastern Hokkaido, Japan, with remarks on the evolution of the genus

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ABSTRACT

A new species of the genus *Bathymodiolus* (sensu lato) is herein described from the lower Oligocene Nuibetsu Formation in eastern Hokkaido, Japan. This is the oldest species of this genus in Japan and the second oldest world wide. Based on occurrence and distribution of fossil *Bathymodiolus* (sensu lato), we suggest that the "genus" spread to the whole world by the late Miocene. This dispersal pattern is supported by molecular studies and similar to that of the large vesicomyids.

Additional keywords: Oligocene, fossil, biogeography, Mytiloidea

INTRODUCTION

Bathymodiolus (sensu lato) is one of the representative members of chemosynthetic communities frequently found at hydrothermal vents and cold seeps. Phylogenetic relationships between *Bathymodiolus* (sensu lato) and other modioline mussels are of considerable interest, since Distel et al. (2000) hypothesized that *Bathymodiolus* (sensu lato) in the seep and vent sites originated from small wood- or bone-associated modiolines. The recent description of *Vulcanidas* from a shallow vent site by Cosel and Marshall (2010) suggests that pathways of adaptation occurred at least three times in the bathymodiolines. It is necessary to examine such pathways of adaptation from the view point of the fossil record.

Six Recent species of this genus are known around Japan (Sasaki et al., 2005). Morphologically, the genus can be classified into the four groups *Bathymodiolus thermophilus*, *B. brevior*, *B.heckerae*, and *B. childressi* (see Cosel, 2002). Most molecular studies, however, indicate that the genus is not a monophyletic group but includes instead several distinct clusters (e.g., Miyazaki et al., 2004; Jones et al., 2006; Iwasaki et al., 2006; Samadi et al., 2007; Fujita et al., 2009). Based on these studies and their morphological data, Cosel and Janssen (2008) recognized the following three clades, the *B. thermophilus*, *B. aduloides*, and *B. childressi* clades. Moreover, the *B. childressi* clade was subdivided into six groups, including the genus *Gigantidas* Cosel and Marshall, 2003 as one group. Among them, the *B. thermophilus* clade includes *B. thermophilus*, *B. brevior*, *B.heckerae* groups of Cosel (2002). Recently, Miyazaki et al. (2010) examined COI and ND4 genes and divided *Bathymodiolus* into four groups that correspond to three clades of Cosel and Janssen (2008) and one clade of the genus *Tamu* Gustafson, Turner, Lutz, and Vrijenhoek, 1998. Very recently, Lorion et al. (in press) also suggested that Bathymodiolinae should be split into the *B. thermophilus* and *B. childressi* groups, based on the studies of COI mtDNA and 28S rRNA. As a conclusion, the genus *Bathymodiolus* is not a monophyletic group, but consists of two or three clades. Strictly speaking, the genus *Bathymodiolus* should be used only for the molecular clade including the type species, *B. thermophilus* Kenk and Wilson, 1985. However, some authors used *Bathymodiolus* (sensu lato) to the clades other than *B. thermophilus* clade (e.g., Cosel and Janssen, 2008; Kiel et al., 2010). In this paper, we use *Bathymodiolus* (sensu lato) for all species hitherto described as *Bathymodiolus*.

The fossil record of *Bathymodiolus* (sensu lato) can be traced back to *B. willapaensis*, which dates from the middle Eocene (Kiel, 2006). In Japan, only three certain and two doubtful fossil records of *Bathymodiolus* (sensu lato) are known from cold-seep sites. One of these records is from the middle Miocene Akanuda Limestone of the Bessho Formation in central Nagano Prefecture. Kuroda (1931) described *Tamarindiformis akanudaensis* as a new species from Akanuda, Matsumoto City. Then, Tanaka (1959) illustrated this species as *Volsella*. Recently, Nobuhara et al. (2008) mentioned that the species possibly belongs to the bathymodiolines, based on the morphology of its juvenile shell. This species has been also illustrated from a large seep carbonate of the uppermost middle Miocene Ogaya Formation in Niigata Prefecture (Amano et al., 2010). "*Bathymodiolus*" sp. has been obtained and illustrated from siltstone of the

Pliocene Tamari Formation in Shizuoka Prefecture by Nobuhara (2003). In addition to these records, Katto and Masuda (1978) illustrated one specimen from the carbonate of the Oligocene(?) Muro Group in Wakayama Prefecture as *Modiolus* sp. This species occurred in association with *Conchocele* cf. *nipponica* (Yabe and Nomura, 1925) and *Callista* cf. *hanzawai* (Nagao, 1928) (= probably not *Callista*, but a vesicomyid). Moreover, Amano et al. (2004) found several specimens of *Bathymodiolus*? sp. in mudstone of the middle Miocene Higashibessho Formation in Toyama Prefecture.

Fortunately, we could collect many bathymodioline specimens of a new species from an Oligocene deposit in Urahoro-cho, eastern Hokkaido. This is the oldest record in Japan at the moment. In this paper, we describe it and discuss its biogeographic significance and evolutionary trend of *Bathymodiolus* (sensu lato).

MATERIALS

The new species described herein is from limestones of the lower Oligocene Nuibetsu Formation which crops out along the Atsunai River, 1.5 km east of Kami-Atsunai railway station in Urahoro-cho, eastern Hokkaido (Figure 1). The limestone can be subdivided into three parts from bottom to top; limestone yielding many fossils and mudstone breccias (10m thick), laminated limestone without fossils (2 m thick) and limestone yielding pebbles of slate, plant debris and fossils (4 m thick). Carbonate minerals of the lower limestone precipitated in an early diagenetic stage are depleted in ^{13}C ($\delta^{13}C$ values as low as –49‰ vs. PDB; Pee Dee Belemnite standard), which indicates methane seep activity (Peckmann and Thiel, 2004). Although both lower and upper parts yield chemosynthetic bivalves, and carnivore or scavenging gastropods, *Bathymodiolus* (sensu lato) was collected only from the parts, in association with the thyasirid *Conchocele bisecta* (Conrad, 1849), the vesicomyid *Hubertschenckia ezoensis* (Yokoyama, 1890), the solemyids *Acharax* aff. *gigas* (Kanno, 1960), *A.* sp., the naticid *Euspira meisensis* (Makiyama, 1926) and the buccinid *Colus* cf. *fujimotoi* Hirayama, 1955. Terminology of description follows Gustafson et al. (1998). All specimens are stored at the Joetsu University of Education (JUE).

SYSTEMATICS

Family Mytilidae
Genus *Bathymodiolus* Kenk and Wilson, 1985

Type Species: *Bathymodiolus thermophilus* Kenk and Wilson, 1985 from hydrothermal vent fields on the Galapagos Rift.

Bathymodiolus (sensu lato) *inouci* new species
(Figures 2–6, 9, 11, 12)

Diagnosis: A small-sized *Bathymodiolus* (sensu lato) with elongate shell, beak near anterior end, nearly straight dorsal and ventral margin; blunt ridge running from umbo to posterior corner.

Description: Shell of small size for genus, up to 45.4 mm long, modioliform, elongate (height/length ratio = 0.30–0.59; length/height ratio = 1.71–3.31), equivalve and inequilateral, moderately inflated, sculptured by growth lines only. Blunt ridge running from beak to posteroventral corner. Beak prosogyrate, situated near anterior end (position of umbo; 2.3–6.9 % of shell length from anterior end). Anterior margin broadly

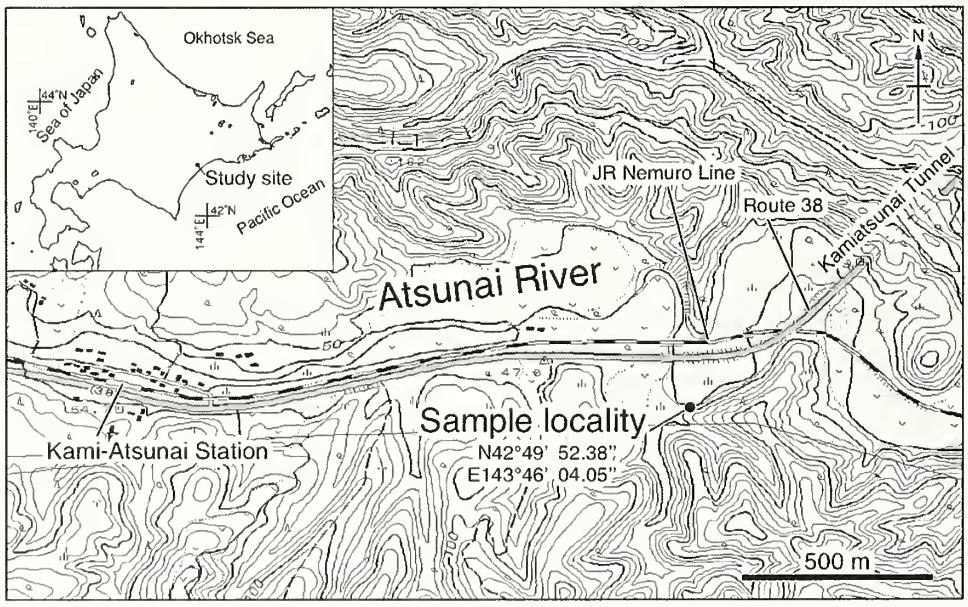
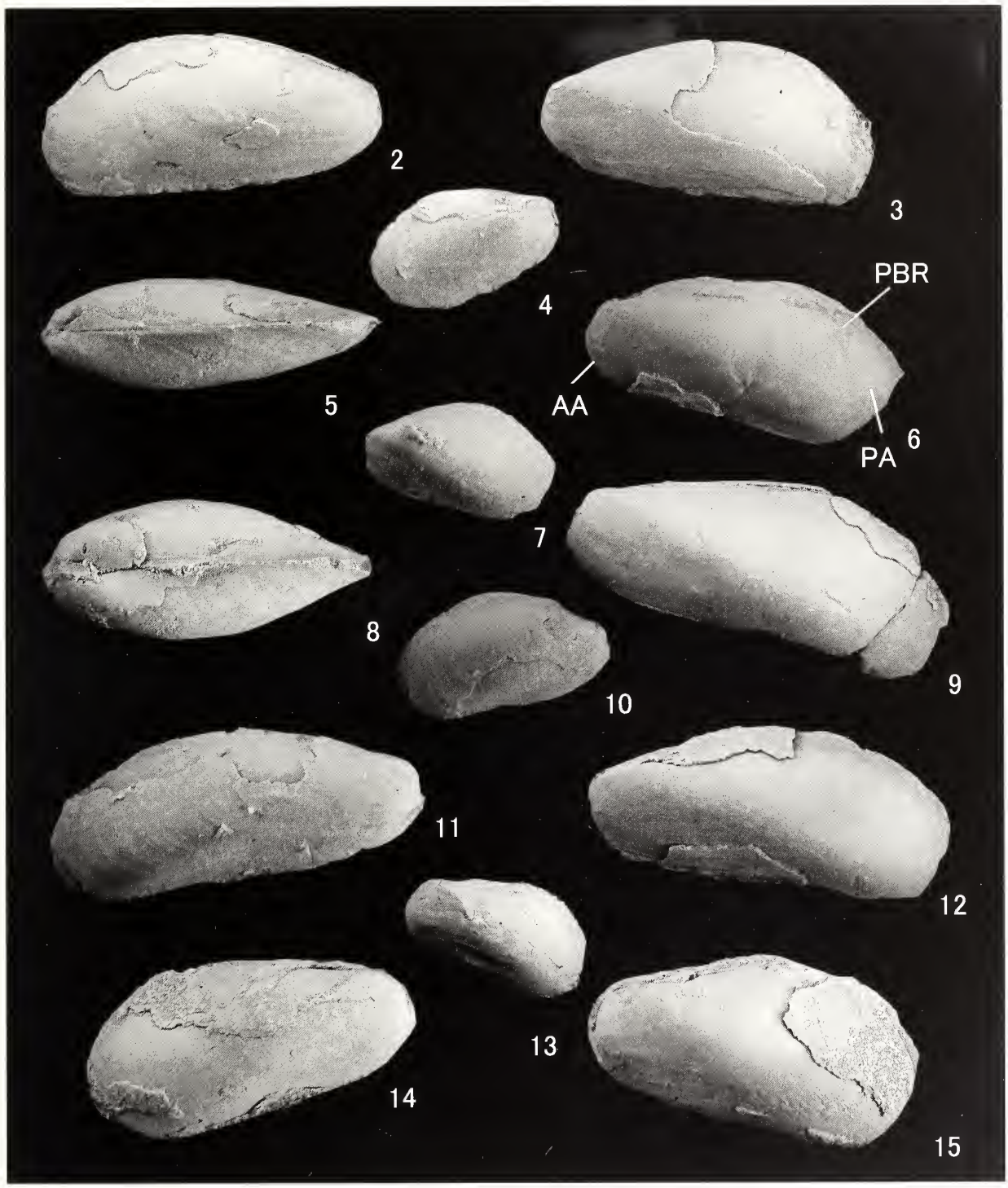


Figure 1. Locality map.



Figures 2–6, 9, 11, 12. *Bathymodiolus* (sensu lato) *inouei* new species. All specimens from type locality. **2, 3, 5.** Holotype, length 28.7 mm, JUE no. 15873. **2.** Right valve. **3.** Left valve. **5.** Dorsal view. **4.** Paratype, length 8.7 mm, JUE no. 15874-5, right valve (juvenile). **6.** Paratype, length 28.4 mm, JUE no. 15874-4, left valve; AA, anterior adductor scar; PA, posterior adductor scar; PBR, posterior byssal retractor scar. **9.** Paratype, length 30.5 mm, JUE no. 15874-3, left valve. **11.** Paratype, length 30.8 mm, JUE no. 15874-1, right valve. **12.** Paratype, length 31.1 mm, JUE no. 15874-2, left valve. **Figures 7, 10.** *Bathymodiolus* (sensu lato) *willapaensis* (Squires and Goedert). Topotype from Bear River deposit, Washington State, USA, collected by RJ. **7.** Length 11.8 mm, JUE no. 15876-1, left valve. **10.** Length 13.8 mm, JUE no. 15876-2, right valve. **Figures 8, 13–15.** *Bathymodiolus* (sensu lato) *akanudaensis* (Kuroda). **8, 14, 15.** Topotype specimens. **8.** Length 29.6 mm, JUE no. 15882-1, dorsal view; **14.** Length 22.4 mm, JUE no. 15882-3, right valve. **15.** Length 24.2 mm, JUE no. 15882-2, left valve. **13.** Length 15.4 mm, JUE no. 15883, left valve, loc. Kita-Kuroiwa, Joetsu City.

arched; ventral margin nearly straight; posterodorsal margin very broadly arched, continuing into steeply sloping posterior margin. Hinge edentulous. Nymph extending from beak and occupying 55% of dorsal margin. Anterior adductor muscle scar distinct, small and semicircular; posterior adductor scar large and ovate; posterior byssal retractor scar long, thin, united with posterior adductor scar.

Holotype: JUE no. 15873.

Paratypes: JUE no. 15874-1 to JUE no. 15874-5; all from the type locality.

Type Locality: Outcrop along the Atsunai River, 1.5km east of Kami-Atsunai Railway Station in Urahoro-cho, eastern Hokkaido.

Material Examined: Eighty specimens were examined. Among these, forty-six are articulated.

Measurements: See Table 1.

Remarks: The new species can be identified as *Bathymodiolus* (sensu lato) because of its modioliform shape and the occurrence from the cold seep site. Owing to its terminal umbo and its continuous posterior retractor scar united posterior muscle scar, the new species may be assigned to the *B. childressi* clade by Cosel and Janssen (2008).

Comparison: The Eocene species *Bathymodiolus willapaensis* (Squires and Goedert, 1991) (Figures 7, 10) has very similar outline to juvenile form of the present species, but has much smaller (27 mm long) and higher shell than *B.* (sensu lato) *inouei* new species (figure 16). Also, *B. akanudaensis* (Kuroda, 1931) from the Miocene Bessho and Ogaya Formations (Figures 13–15) can be discriminated by having distinctly higher and more inflated shell than the new species (Figures 16, 17). *Bathymodiolus* (sensu lato) *inouei* resembles *Bathymodiolus* (sensu lato) *palmarensis* Kiel, Campbell and Gaillard, 2010, from the "Oligocene" deposit of Colombia, in its elongated shell and its beak located near anterior end, but differs from it by having less distinct ridge and less expanded posterior part. *Volsella yokoyamai* Hatai and Nisiyama, 1952 described from the upper Eocene Iwaki Formation in Fukushima Prefecture resembles *B.* (sensu lato) *inouei* in having an elongate shell, but differs by its well inflated shell, more posteriorly located beak and more distinct ridge. One specimen illustrated by

Table 1. Measurements of *Bathymodiolus* (sensu lato) *inouei* new species.

Specimens	Type	Length (mm)	Height (mm)	H/L	L/H	Anterior length (mm)	Position of umbo (%)	Width (mm)
JUE no. 15873	Holotype	28.7	13.3	0.46	2.16	1.6	5.6	9.1
JUE no. 15874-1	Paratype	30.8	12.0	0.39	2.57	1.4	4.5	10.1
JUE no. 15874-2	Paratype	31.1	13.4	0.43	2.32	0.7	2.3	9.8
JUE no. 15874-3	Paratype	30.5	12.3	0.40	2.48	2.1	6.9	8.7
JUE no. 15874-4	Paratype	28.4	14.4	0.51	1.97	1.5	5.3	9.7
JUE no. 15874-5	Paratype	8.7	5.1	0.59	1.71	0.5	5.7	3.0
JUE no. 15875-1	Topotype	45.4	13.7	0.30	3.31	-	-	-
JUE no. 15875-2	Topotype	29.1	13.6	0.47	2.14	0.8	2.7	9.3
JUE no. 15875-3	Topotype	30.2	12.4	0.41	2.44	0.7	2.3	-
JUE no. 15875-4	Topotype	27.7	12.4	0.45	2.23	1.5	5.4	8.6
JUE no. 15875-5	Topotype	24.2	12.3	0.51	1.97	1.1	4.5	6.6
JUE no. 15875-6	Topotype	25.0	11.6	0.46	2.16	1.3	5.2	-
JUE no. 15875-7	Topotype	24.7	10.7	0.43	2.31	1.3	5.3	-
JUE no. 15875-8	Topotype	27.1	12.2	0.45	2.22	1.3	4.8	8.8
JUE no. 15875-9	Topotype	27.0	12.9	0.48	2.09	1.2	4.4	9.3
JUE no. 15875-10	Topotype	23.4	10.5	0.45	2.23	1.1	4.7	-
JUE no. 15875-11	Topotype	21.2	9.7	0.46	2.19	1.0	4.7	-
JUE no. 15875-12	Topotype	20.4	10.0	0.49	2.04	1.4	6.9	6.5
JUE no. 15875-13	Topotype	19.8	9.2	0.46	2.15	0.8	4.0	6.7
JUE no. 15875-14	Topotype	18.8	10.2	0.54	1.84	1.2	6.4	6.7
JUE no. 15875-15	Topotype	19.2	9.1	0.47	2.11	-	-	6.1
JUE no. 15875-16	Topotype	17.8	8.0	0.45	2.22	1.1	6.2	5.2
JUE no. 15875-17	Topotype	16.3	9.1	0.56	1.79	0.7	4.3	4.9
JUE no. 15875-18	Topotype	13.8	6.7	0.49	2.06	0.7	5.1	4.3

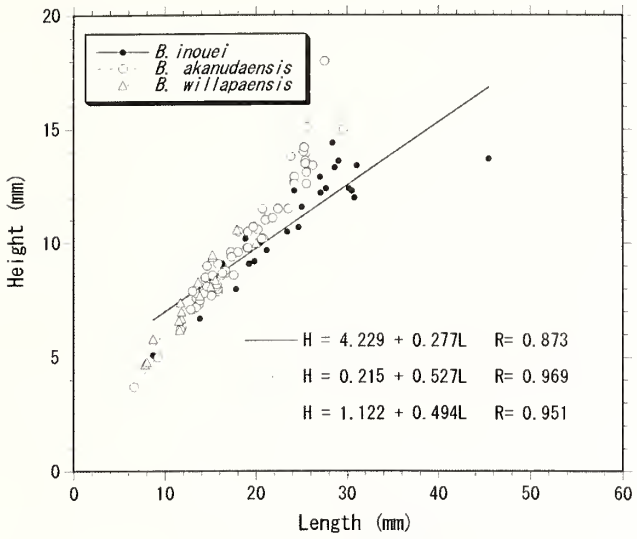


Figure 16. Ontogenetic changes in shell length and height of *Bathymodiolus* (sensu lato) *inouei*, *B.* (sensu lato) *willapaensis* and *B.* (sensu lato) *akanudaensis*.

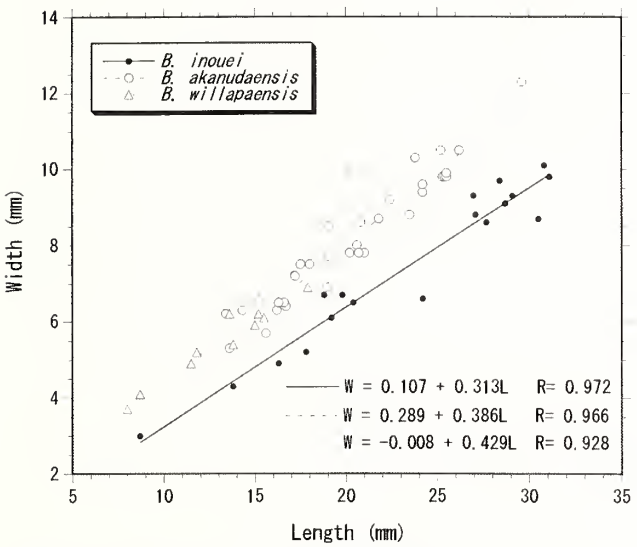


Figure 17. Ontogenetic changes in shell length and width of *Bathymodiolus* (sensu lato) *inouei*, *B.* (sensu lato) *willapaensis* and *B.* (sensu lato) *akanudaensis*.

Katto and Masuda (1978) as *Modiolus* sp. from the Oligocene? Muro Group in Wakayama Prefecture may be inferred as *Bathymodiolus* (sensu lato) by the occurrence from the carbonate in association with chemosynthetic species. This specimen is similar to the new species in its shell outline. However, owing to a few data on its specimen, it is necessary to collect additional specimens for comparing with this new species in detail.

Distribution: Known only from type locality. Lower Oligocene Nuibetsu Formation in Hokkaido.

Etymology: Named after Mr. Kiyokazu Inoue, Obihiro City, an amateur collector of molluscan fossils, who found the locality of this new species.

DISCUSSION

Only four Paleogene species of *Bathymodiolus* (sensu lato) are presently known. Among them, *B. willapaensis* is the oldest species, having been reported from middle Eocene to late Oligocene seep carbonates in Washington State, USA (Goedert and Squires, 1990; Squires and Goedert, 1991; Goedert and Squires, 1993; Goedert and Campbell 1995; Kiel, 2006). Probably, the next oldest record is the present new species from the lower Oligocene. Kiel et al. (2010) described *B. palmarensis* from the "Oligocene" in Colombia, but its precise age is uncertain. Moreover, one specimen was illustrated as *Modiolus* sp. from the Oligocene? Muro Group in Wakayama Prefecture, central Honshu by Katto and Masuda (1978). All Paleogene species are small (less than 50 mm) and have their beak located near the anterior end which is one of the diagnostic features of *Bathymodiolus childressi* clade.

In contrast, many records of *Bathymodiolus* (sensu lato) are known from the Neogene deposits around the world. *Bathymodiolus akanudaensis* and *B.*? sp. occur in a middle Miocene deposit in central Honshu (Kuroda, 1931; Tanaka, 1959; Nobuhara et al., 2009; Amano et al., 2004, 2010). In the Caribbean area, two bathymodioline species have been described from the Miocene Freeman's Bay Limestone of the late middle Miocene Lengua Formation in Trinidad and from the lower to middle Miocene Husto Clay Member of the Pozon Formation in Venezuela (Gill et al., 2005). *Modiolus* (*Modiolus*) *exbrochii exbrochii* Sacco and an elongate *Bathymodiolus*-like fossil were reported from the upper Miocene "Carcari a *Lucina*" at Montepetra, Italy (Moroni, 1965; Taviani, 1994, 2001). Recently, Saether et al. (2010) described *Bathymodiolus* (sensu lato) *heretaunga* and *Gigantidas coseli* as new species from the ?late early to the earliest late Miocene in the North Island of New Zealand. Of Pliocene age is "*Bathymodiolus*" sp. reported by Nobuhara (2003) from siltstone of the Tamari Formation in the forearc basin of Honshu.

Considering the geographic distribution of these records, we suggest that the worldwide spread of *Bathymodiolus* (sensu lato) might occur by the late Miocene (Figure 18). This trend of geographic spread is the same to that of the large vesicomyids which is another characteristic taxa of chemosynthetic fauna (Taviani, 2001; Gill et al., 2005; Lucentte and Taviani, 2005; Amano and Kiel, 2007; Amano and Kiel, in press; Kiel and Peckmann, 2007; Campbell et al., 2008; Kiel and Amano, 2010). Moreover, this pattern is consistent with the molecular study of Miyazaki et al. (2008), who estimated that the worldwide spread of *Bathymodiolus* (sensu lato) took place during the middle Miocene.

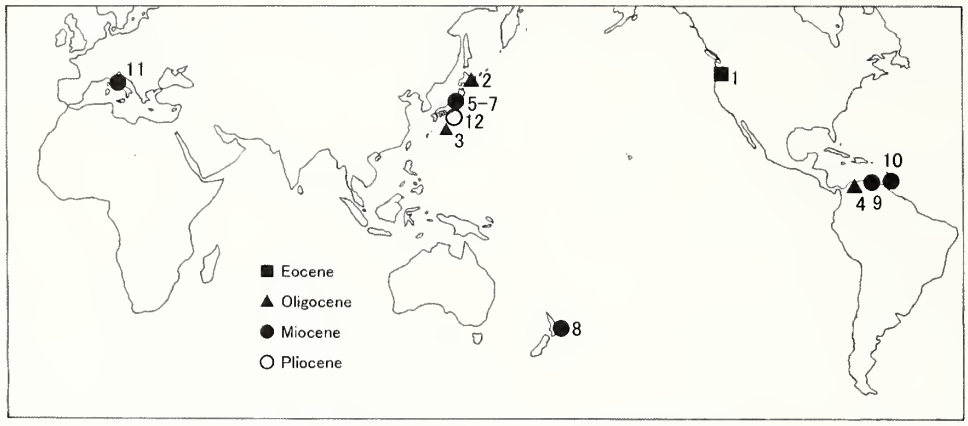


Figure 18. Distribution of the fossil *Bathymodiolus* (sensu lato). 1. *B. willapaensis* (Goedert and Squires, 1990; Squires and Goedert, 1991; Goedert and Squires 1993; Goedert and Campbell 1995; Kiel, 2006); 2. *B. inouei* (this study); 3. *Modiolus* sp. (Katto and Masuda, 1978); 4. *B. palmarensis* (Kiel et al., 2010); 5. *B. akanudaensis* (Kuroda, 1931; Tanaka, 1959; Nobuhara et al., 2009); 6. *B. akanudaensis* (Amano et al., 2010); 7. *B.*? sp. (Amano et al., 2004); 8. *Bathymodiolus* (sensu lato) *heretaunga* and *Gigantidas coseli* (Saether et al., 2010); 9. Venezuela bathymodioline (Gill et al., 2005); 10. Trinidad bathyodiolin (Gill et al., 2005); 11. *Modiolus* (*Modiolus*) *exbrochii exbrochii* Sacco (Moroni, 1965; Taviani, 1994, 2001); 12. "*Bathymodiolus*" sp. (Nobuhara, 2003).

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Dillwynella voightae new species, a new skeneimorph gastropod (Turbinidae) from the western Atlantic and a new record of *Dillwynella modesta* (Dall, 1889)

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ABSTRACT

Dillwynella is a marine gastropod genus found on natural wood falls and sunken algal holdfasts in the Caribbean Sea and the Pacific Ocean. *Dillwynella voightae* new species from the Gulf of Mexico was the second species found in the Atlantic. Previously known only from two localities in the Caribbean Sea, *D. modesta* (Dall, 1889) has now been recorded at a third site, off southeastern Brazil.

Additional keywords: Bathyal, deep sea, Skeneidae, wood fall

INTRODUCTION

Dillwynella modesta (Dall, 1889) was originally described as *Teinostoma* (*Dillwynella*) *modesta* (Dall, 1889a), in the family Trochidae. Later in the same year, Dall changed the status of *Dillwynella* to a full genus within the Trochidae (Dall, 1889b). The species was described from off St. Lucia (13°51.30′ N, 61°03.45′ W; Smith, 1889: 968), on coarse sand at a depth of 413 meters (Dall, 1889a). Marshall (1988) mentioned that at the same station the wood ingesting limpet *Pectinodonta arcuata* Dall, 1882 was also found, therefore both species may have lived originally on wood (Marshall, 1988). A second record of 5 specimens of *D. modesta* from off the coast of Georgia, USA (Dall, 1927) was given, but the specimens are mostly immature (Dall, 1927) and, according to Warén (pers. com.), in a very bad condition. Nowadays, the genus *Dillwynella* is referred to the subfamily Skeneinae, family Turbinidae (Marshall, 1988; Bouchet & Rocroi, 2005). Williams and Ozawa (2006) placed the Turbinidae inside the vetigastropod superfamily Troehoidea. This is the third record of *D. modesta* since the type lot was recorded. It is the first time that this species has been found south of the Caribbean Sea.

Marshall (1988) described *Dillwynella lignicola*, *Dillwynella haptricola*, and *Dillwynella ingens* from the New Zealand region. Hasegawa (1997) added the following four species from the Suruga Bay to this genus: *Dillwynella vitrea*, *Dillwynella planorbis*, *Dillwynella fallax* and *Dillwynella sheisinmaruae*. Macrophotographs of the species described by Hasegawa are illustrated in Okutani (2000: 84–85). All these species of *Dillwynella* were associated with sunken wood, except *Dillwynella haptricola* Marshall, 1988, which lives on sunken algal holdfast (Marshall, 1988) in depths of 529–1200 m.

Ganesa panamensis Dall, 1902 may be a ninth species included in the genus *Dillwynella*. It was found in the Gulf of Panama at a depth of 1865 meters in mud and has never been found outside this type locality. In his description and figure five years later, Dall (1902; 1908) recorded the genus with a question mark and stated his uncertainty about the status of *Ganesa*. The shell figured (Dall, 1902: pl. 19, fig. 4) resembles that of a *Dillwynella* species. If it were to be reclassified within *Dillwynella*, not only it would be the first species of this genus found in the eastern Pacific, but would also be the deepest occurring one.

Dillwynella voightae new species is the second species of this genus described from the Atlantic region.

MATERIALS AND METHODS

The specimens were fixed in formaldehyde and preserved in ethanol. Pictures of the shells with soft parts in ethanol and of the dried shell were taken with a

macro objective and digital camera. After drying of the specimen, the body was pushed into the shell gently, with a needle, to disconnect the columellar muscle. Afterward, the shell with the soft parts was rehydrated in a solution of water and very little dishwashing liquid. With a hooked needle, the body was then pulled out of the shell (Geiger et al., 2007). For the scanning electron microscope (SEM), the rehydrated soft parts were critical-point dried. To facilitate acquisition of more information on the soft parts, the mantle roof was removed after the first SEM session and mounted separately. Both the soft parts (without the mantle roof) and the mantle roof itself were examined again under SEM. After image-acquisition of the body under SEM, the head-food was dissolved in KOH and the radula cleaned and mounted for SEM. For the SEM of the shell (paratype), the operculum and the radula were air dried. All SEM specimens were coated twice with gold from different orientation, for 180 seconds.

Institutional abbreviations used are: FMNH: The Field Museum of National History, Chicago, USA; MNHN: Muséum National d'Histoire Naturelle, Paris, France; and USNM: National Museum of Natural History, Washington, DC, USA.

SYSTEMATICS

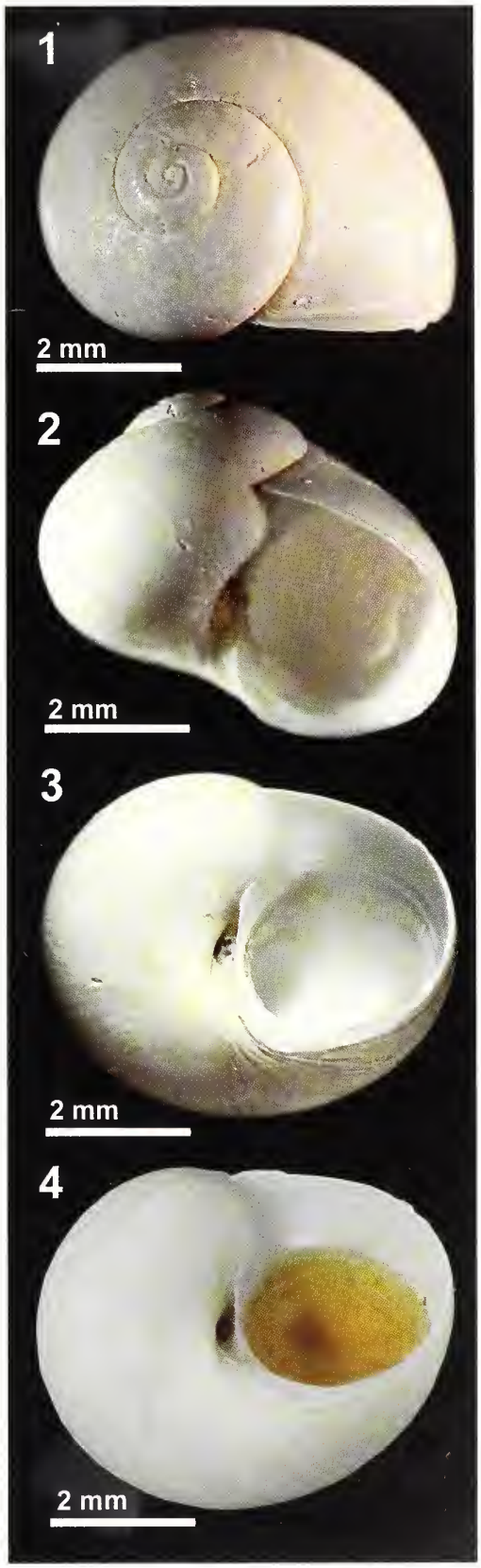
Family Turbinidae Rafinesque, 1815
Subfamily Skeneinae Clark, 1851
Genus *Dillwynella* Dall, 1889

Type Species: *Dillwynella modesta* (Dall, 1889) (by subsequent lectotype designation of Marshall, 1988)

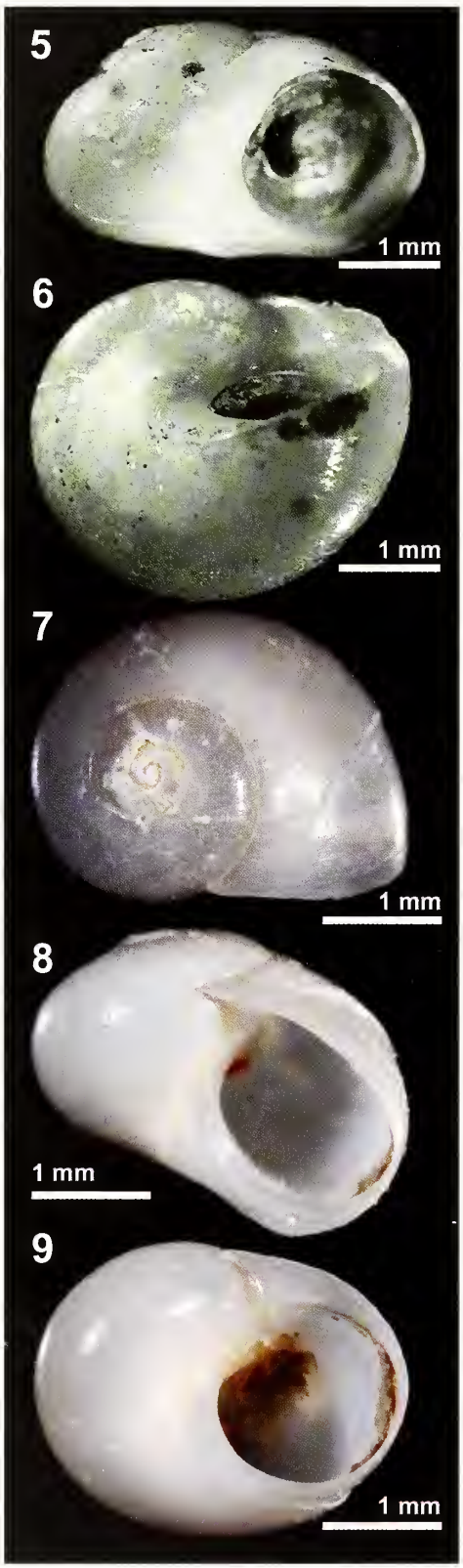
Dillwynella voightae new species
(Figures 1–4, 10–20)

Description: Protoconch (paratype, Figures 10–11): Most specimens badly corroded. Pictures of protoconch (Figure 11) are taken from a juvenile specimen (shell diameter = 1.5 mm). Protoconch 390 µm maximum diameter, 0.5 whorls, covered by a thick deposit, hiding all structures. Teleoconch (holotype, Figures 1–4): Adult shell with 2.7 whorls, large (diameter 5.8 mm, height 4.8 mm), rather thin and fine, color pure white. Teleoconch smooth, except for growth lines, which are prosocline and cover entire teleoconch. Suture distinct and narrow, getting a little deeper on first half whorl. First quarter of apical telcoconch whorl with a median, strong, spiral rib starting quite strong at the border of protoconch and teleoconch, fading out and disappearing (Figure 11). Umbilicus a narrow chink, demarcated by inner lip, distinct, elongated, oval, and deep. Aperture moderately D-shaped. Parietal callus thin. Lower part of the outer lip broad. Parietal glaze thin.

Operculum (Holotype, Figures 4, 12): Diameter 2.8 mm, multispiral, moderately thick, short growth edge; yellow, partly brownish, translucent at outer edge.



Figures 1–4. *Dillwynella voightae* new species (holotype, FMNH 312467, Gulf of Mexico, 5.8 mm width).



Figures 5–9. *Dillwynella modesta* (Dall, 1889). **5–6.** Lectotype (USNM 859220, off St. Lucia, 3.9 mm width). Photos by A. Warén. **7–9.** MNHN unnumbered, off southeastern Brazil, 3.1 mm width).

Radula (Holotype, Figures 16–18): Formula n-5-1-5-n, length 3.5 mm, width 300 µm. Central tooth large, with broad and smooth cutting edges, shaft reduced to a low ridge, not hooked at tip. Lateral teeth longer than broad, outer teeth getting larger, S-shaped, tip strongly hooked, cutting area long and smooth. Marginal teeth slender, elongated and simple, with smooth edge, strongly hooked at tip. Third to fourth marginal teeth longest, getting shorter and narrower laterally. Jaws present, with prismatic elements, thin (Figure 20).

Gross Anatomy (Holotype, Figure 13–15): Body flesh-colored; snout broad and flat; cephalic tentacles broad at basis, getting long and slender at tip, with sensory papillae. Large, V-shaped propodium. [Due to drying and rehydration of soft parts, small structures like eye-stalks and suboptic tentacles were stuck together and could not be seen.] Four epipodial tentacles on each side of mesopodium. Three epipodial tentacles, relatively short, conical shaped with laterally placed sensory papillae. First one has attached a small accessory tentacle, which is smooth and small, without sensory papillae (epipodial sense organ). Large number of sensory papillae present on mantle edge and mantle roof. [Attempts to separate the mantle roof from the soft parts caused exposure of gut contents, which consisted of wood fibers (Figure 19).

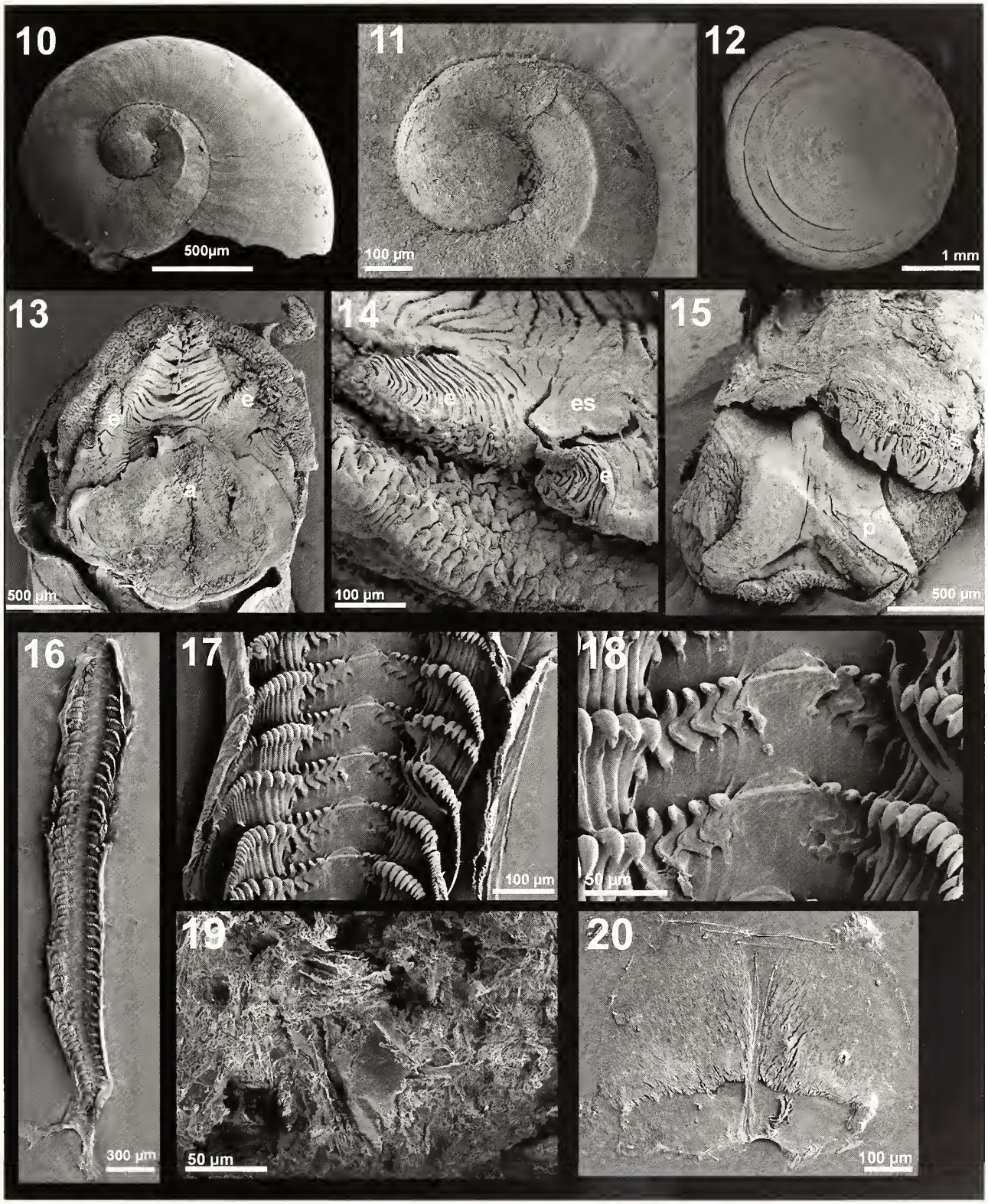
Type Material: Holotype: A dried shell, FMNH 312467 (Figures 1–4, 12–20). Paratypes: 16 specimens in ethanol, FMNH 312220, 1 juvenile shell dried, used for SEM pictures of the protoconch, FMNH 312468 (Figures 10–11).

Type Locality: North Atlantic, Gulf of Mexico, Louisiana, U.S.A. (27°44.09′ N, 91°14.49′ W), natural wood fall, 610 m depth. The sample was taken by the grab of the DSV Johnson-Sea Link I (operating from R/V Seward Johnson), 19 Aug. 2006.

Material Preservation: The specimens were fixed in formalin and stored afterward in 70% ethanol.

Etymology: Named after Dr. Janet R. Voight, Field Museum of Natural History, who collected the specimens.

Comparative Remarks: *Dillwynella voightae* new species is the largest described species of this genus. The teleoconch resembles *Dillwynella vitrea* Hasegawa, 1997, *D. haptricola* Marshall, 1988, and *D. modesta* (Dall, 1889). These four species have a distinct, median strong spiral rib on the beginning of the protoconch and have no ribs in the area around the umbilicus. *Dillwynella vitrea*, *D. haptricola*, and *D. voightae* differ by the shape of their umbilicus. *Dillwynella vitrea* has a distinct big umbilicus, whereas *D. voightae* shows a narrow chink, and *D. haptricola* a small chink almost closed by its thin inner lip. *Dillwynella modesta* (Figures 5–9; SEM images: Marshall, 1988: fig. 2: D–E) differs by lacking an umbilicus.



Figures 10–20. *Dillwynella voightae* new species. **10–11.** Juvenile specimen shell (paratype, FMNH 312220, shell 2.9 mm width). **10.** Shell. **11.** Protoconch of juvenile specimen shell. **12–20.** Holotype (FMNH 312467, 5.8 mm width). **12.** Operculum. **13.** Ventral view of foot. **14.** Epipodial tentacles and epipodial sense organs. **15.** Lateral view of soft parts with propodium and snout. **16–18.** Radula. **19.** Gut content. **20.** Jaw. Abbreviations: **a,** attachment area of the operculum; **e,** epipodial tentacle; **es,** epipodial sense organ; **s,** snout; **p,** propodium.

Distribution: Known only from type locality.

Remarks: The wood fibers in the gut show that *D. voightae* feeds directly on wood and grazes not only on the bacteria film.

Dillwynella modesta (Dall, 1889)

Type Material: Lectotype: A dried shell, USNM 859220 (Marshall, 1988; originally syntype USNM 95077, after Dall, 1889a), illlustrated in Dall (1889a), macrophotographs (Figures 5–6). Paralectotype: A dried shell, USNM 95077; SEM pictures in Marshall (1988: 958, 993).

Type Locality: St. Lucia at BLAKE Station 205 coarse sand in 413 meters depth.

Material Examined: Two dry specimens, one empty shell, and one shell with soft parts, MNHN (Figures 7–9), off southeastern Brazil (23°47′ S, 42°10′ W), N.O. MARION DUFRESNE, Cruise MD 55, Bouchet, Leal, and Métivier coll. May 1987, sta. CB105, 610 m depth.

Distribution: Western Atlantic from Gulf of Mexico to Brazil, but only known from three localities.

Remarks: The specimens of *Dillwynella modesta* found off Brazil (Figures 7–9) are quite similar to the types. This is the second finding of this species and shows its wide distribution. Unfortunately, there are no data available for the substrate of the specimens.

DISCUSSION

The presence of an epipodial sense organ at the base of the papillate epipodial tentacles, described by Crisp (1981) and histology shown for microgastropods in Kunze et al. (2008), underlines the position of this genus in the Trochoidea/Turbinoidea (Bouchet and Rocroi, 2005). To solve its precise position in this group and confirm the position in the Skeneinae more information like microanatomy or sequencing are needed. The new record of *Dillwynella modesta* shows its wide occurrence in the western Atlantic. It also demonstrates how rare and incomplete the records of sunken wood species are in this area.

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Research Note

The first confirmed record of the Chinese Pond Mussel (*Sinanodonta woodiana*) (Bivalvia: Unionidae) in the United States

The Chinese Pond Mussel, *Sinanodonta woodiana* (Lea, 1834) (previously referred to as *Anodonta woodiana*), is a widely introduced unionid around the world. There is evidence that *Anodonta* from China were imported into Asian markets in the western United States as early as the late 1800s (Wood, 1892), but were not known to have been released in open waters. Watters (1997) surveyed the countries where this nonindiginous species had been documented as established and reported them from France, Hungary, Romania, Indonesia, Costa Rica, and the Dominican Republic. The native range of this species was reported to be eastern Russia, China, Cambodia [doubtful], Thailand [this is refuted by Brandt (1974)], Malaysia [it is claimed by Brandt (1974) to have been imported to several Malaysian localities by Chinese fish breeders] and Taiwan. Watters (1998, 1999) added Singapore, the Philippines, and possibly Panama to the list of countries where this species has been introduced.

Watters (1997) noted the absence of *Sinaondonta woodiana* records for the United States but pointed out that it might be confused with the native species of *Anodonta* of similar size and shape, *Anodonta suborbiculata* or *Anodonta* sp., subsequently described as *A. hartfieldorum*. Watters observed that "Given the history of this species' invasion elsewhere, and the continued farming and exporting [importing] of its hosts, it is likely that *A. woodiana* eventually will invade North America and other countries."

Information on the range expansion of the Chinese Pond Mussel across Europe has been continuously updated by Mienis (1999, 2001, 2002a–c; 2003, 2004a, b; 2005, 2006a–c; 2007a, b; 2008a, b; 2009a, b; 2010), documenting the occurrence of this invasive mussel as it spread across 15 countries in Europe: Austria, Belgium, Bulgaria, France, Greece, Hungary, Italy, Moldova, Poland, Romania, Serbia, Slovakia, Sweden, the Netherlands, and Ukraine. Distribution information for France and Europe including a discussion of colonization hypotheses and ecological threats has been provided by Adam (2010). Bogan and Schilthuizen (2004) reported it from the island of Borneo, Sabah, Malaysia.

Sinanodonta woodiana appears to have been introduced via the release of host fishes infested with glochidia. Watters (1997) listed potential nonindigenous fish hosts including Cyprinidae (minnows): *Achcilgnathus moriokae*, *Metzia takakii*, *Puntius semifasciolatus*, *Rhodeus tabira*, *Zacco platypus*, *Z. temmincki;* and Gobiidae (gobies): *Rhinogobius brunneus*. Fish hosts also include commercially imported cultured fish: Cyprinidae: Bighead Carp (*Hypophthalmichthys nobilis*), Black Carp (*Mylopharyngodon piceus*), Common Carp (*Cyprinus carpio*), Grass Carp (*Ctenopharyngodon idella*), Silver Carp (*Hypophthalmichthys molitrix*); and Cichlidae (cichlids): Nile Tilapia (*Orcochromis niloticus*). One native fish, Poecillidae, (mosquitofishes), Western Mosquitofish, *Gambusia affinis*, is also reported to serve as a glochidial host. Mienis (2002b) noted that Grass Carp and Silver Carp were the probable host fish for *Sinaondonta woodiana* when it was first introduced into Europe in 1983.

Three live specimens of anodontine bivalves suspected to be *Sinaondonta woodiana* were collected from the New Jersey Conservation Foundation's fish ponds, off Joe Ent Road, 3.3 air miles south-southeast of the center of Pittstown, Franklin Township, Hunterdon County, New Jersey by the NJ Endangered and Nongame Species Program staff on 7 June 2010. These specimens were placed directly into 95% ethyl alcohol and sent to the North Carolina State Museum of Natural Sciences, Raleigh, and catalogued (number NCSM 46965) into the Mollusk Collection.

A small mantle snip was taken to be used for DNA analyses. DNA was extracted and a portion of the mitochondrial gene cytochrome oxidase subunit 1 [CO1] was sequenced following protocols outlined in Raley et al. (2006). A BLAST search (Zhang et al, 2000) was performed with these sequences which confirmed their identification as *Sinanodonta woodiana*. These same sequences were inserted into our data matrix of anodontine bivalves where it clustered with two other specimens of *S. woodiana* and was sister to *Anodonta beringiana*. Genetic data and shell characters appear sufficient to verify the identity of these samples as *S. woodiana*, confirming the first record of an established population of this highly invasive species in the U.S.

Following the discovery of *Sinaondonta woodiana*, the New Jersey Conservation Foundation staff lowered water in the ponds and killed all fish with Rotenone. Fish removed from the ponds included: Bluegill, Bighead Carp, Common Carp, Grass Carp (diploid), Largemouth Bass, and American Eel. Although the ponds have been lowered, they are fed by runoff and springs and have begun to refill. It is unknown whether live mussels remain in the ponds. Planning is underway to determine the best method of complete eradication at the site. Possible actions include either draining the ponds via pumping or allowing them to freeze over during the winter and then conducting surveys to determine if there are surviving individuals. Shells have been found in Wickecheoke Creek downstream of the ponds at several locations but no live individuals were found. This creek is

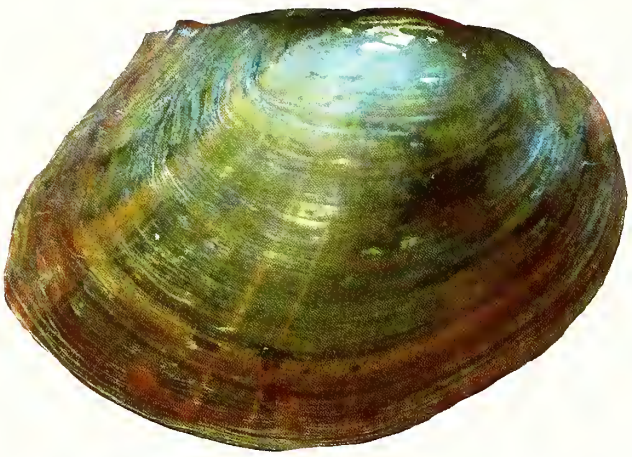

Figure 1. Picture of the shell of one of the specimens collected from fish ponds, Hunterdon County, New Jersey. NCSM 46965-3.

Figure 2. Picture of umbonal sculpture of specimen *Sinanodonta woodiana* NCSM 46965.1.

tributary to Delaware River and also connects to the D & R Canal at Stockton, New Jersey. The occurrence of shells along Wickecheoke Creek and a recent sighting of a relict shell near the D & R canal at Prallsville Mills is evidence that fish bearing Chinese Pond Mussel glochidia may have spread downstream. The extent of the invasion is unclear at this time.

The molecular work presented here is a contribution from the NC State Museum's Molecular Genetics Laboratory.

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Errata

In the last issue (The Nautilus, volume 124, issue number 4), on page 161, right-hand column, two last lines, replace "...and redescribed *Archivesica nipponica* in detail." for "...and redescribed *Archivesica shiretokensis* in detail."

In the same issue (The Nautilus, volume 124, issue number 4), the following authors and page numbers were omitted from the "Index to Authors" (unnumbered page 195 at the end of issue):

Bertsch, H. 188
Fallon, P., Jr. 166
Lyons, W. G. 192
Rosenberg, G. 192
Snyder, M. A. 192

Sponsored in part by the State of Florida, Department of State, Division of Cultural Affairs, the Florida Arts Council and the National Endowment for the Arts.

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New species of Paleogene cypraeoideans (Gastropoda) from the Pacific slope of North America

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ABSTRACT

A new species of *Bernaya* sensu stricto (Cypraeidae) from Eocene rocks of Washington and four new species of *Eocypraea* sensu stricto (Eocypraeidae), one from Paleocene strata of northern California, two from Eocene strata of Washington, and one from Baja California Sur, Mexico, are described. The new species of *Bernaya* sensu stricto and the Washington species of *Eocypraea* sensu stricto represent the northernmost Cenozoic records for their respective genera in western North America. A tentative record of *Eocypraea* (*Eocypraea*) *inflata* (Lamarck, 1802), previously known only from the Lutetian Stage (middle Eocene) of France, Belgium, and England, is noted from the middle Eocene Domengine Formation of Kings County, California.

Additional keywords: Bernaya, Eocypraea, fossils, paleontology, Paleocene, Eocene

INTRODUCTION

Five new species of Paleogene cypraeoideans are described from localities on the Pacific slope of North America (Table 1). The new species of *Bernaya* sensu stricto represents the first record of this genus from Washington and is the northernmost record of the genus in western North America. Four new species of *Eocypraea* sensu stricto are described from strata in Lake County, California, Thurston and Lewis counties, Washington, and Baja California Sur, Mexico. All four species represent first records from their respective regions and the species from Washington are the northernmost representatives of the genus in western North America. These taxa are indicators of shallow, warm water depositional environments.

STRATIGRAPHY AND GEOLOGIC AGES

The formations listed below, from oldest to youngest, are those from which the new species are described. Because these formations have been mentioned by previous authors, only a brief overview of the stratigraphic nomenclature and age will be mentioned. Readers will be referred to additional sources for detailed descriptions.

Martinez Formation

Whitney in Gabb (1869: xiii) provisionally proposed the Martinez Group to "include a series of beds, of small geographical extent, found at Martinez [California] and on the northern flank of Monte Diablo." He also incorrectly noted that the group may eventually prove to be worthy of ranking only as a subdivision of the Cretaceous Chico Group. In the same volume, Gabb (1869: 129) referred to the Martinez Group as "the upper portion of 'Division A' of the California reports." These beds were provisionally demonstrated to be "Paleocene" age by Clark and Vokes (1936). Brice (1953) referred to Paleocene strata in Lake County, California, as Martinez Formation. He noted that "fossils characteristic of the Paleocene Martinez are found in scattered localities through the sandstone, and the lithologic assemblage is similar to that of the type Martinez formation." Therefore, for the lack of a more appropriate name, the usage of Brice will be followed and these uppermost lower or lowermost upper Paleocene (Danian/Thanetian stages) beds in Lake County will be referred to as "Martinez" Formation.

Crescent Formation

The Crescent Formation of Arnold (1906: 460–461) was described for a "series black basalt and greenish basalt tuffs and tuffaceous sands found in the vicinity of Port Crescent," Clallam County, Washington. Weaver (1937) referred to the Crescent Formation as middle Eocene ("Capay" California provincial molluscan stage [CPMS]) tuffaceous shales and sandstones and basaltic agglomerate of marine origin exposed on the northern flank of the Olympic Peninsula. Recently, much confusion has been ascribed to Eocene deposits near Maynard on Discovery Bay. Durham (1944) referred

Table 1. List of the species of *Bernaya (Protocypraea)*, *Bernaya* sensu stricto, and *Eocypraea* sensu stricto from western North America and their generalized localities (formation is included for new species).

***Bernaya (Protocypraea)* and *Bernaya* sensu stricto**

Late Cretaceous

Bernaya (Protocypraea) argonautica (Anderson, 1958) [Jackson Co., Oregon]
B. (P.) berryessae (Anderson, 1958) [Yolo Co., California]
B. (P.) gualalaensis (Anderson, 1958) [Mendocino Co, California]
B. (P.) popenoei Groves, 2004 [Orange Co., California]
B. (P.) rinconi Groves, 1990 [San Diego Co., California]
B. (Bernaya) beardi Groves, 2004 [Vancouver Id., British Columbia]
B. (B.) crawfordcatei Groves, 1990 [San Diego Co., California]
B. (B.) jeanae Groves, 2004 [Butte Co., California]

Eocene

Bernaya (Protocypraca) grovesi Squires and Demetrion, 1992 [Baja California Sur, Mexico]
Bernaya (Bernaya) ***squiresi*** new species [Cresecnt Formation, Jefferson Co., Washington]

***Eocypraea* sensu stricto**

Late Cretaceous

Eocypraca (Eocypraca) louellae Groves, 1990 [Yolo Co., California]

Paleocene

Eocypraca (Eocypraca) novasumma (Nelson, 1925) [Ventura Co., California]
Eocypraca (Eocypraca) ***takeosusukii*** new species ["Martinez" Formation, Lake Co., California]

Eocene

Eocypraca (Eocypraca) ***batequensis*** new species [Batcque Formation, Baja California Sur, Mexico]
Eocypraca (Eocypraca) bayerquei (Gabb, 1864) [Contra Costa Co., California]
Eocypraca (Eocypraca) castacensis (Stewart, 1926 [1927]) [Kern Co., California]
Eocypraca (Eocypraca) ***crescentensis*** new species [Crescent Formation, Thurston Co., Washington]
Eocypraca (Eocypraca) ***jimgoederti*** new species [Crescent Formation, Lewis Co., Washington]
Eocypraca (Eocypraca) cf. *E. (E.) inflata* (Lamarck, 1802) [Kings Co., California]
Eocypraca (Eocypraca) maniobraensis Squires and Advocate, 1986 [Riverside Co., California]

to these beds as Eocene basalts, sandstones, shales, and small limestone lenses. Armentrout and Berta (1977) mentioned Narizian/Refugian benthic foraminiferal stages (late middle to late Eocene) aged foraminifera from a locality within the Townsend Shale Member of the Lyre Formation on the east side of Discovery Bay. Tabor and Cady (1978) mapped outcrops on the west side of Discovery Bay as a "sandstone and minor siltstone member" of the Lyre Formation, a younger unit than the Crescent Formation. Armentout and others (1983) referred to these beds as "sandstone of Maynard" and proposed that it interfingers with the lower to middle Eocene upper Crescent Formation. Most reeently Speneer (1984) mapped the area as a "sedimentary member" of the Crescent Formation.

Domengine Formation

Anderson (1905) deseribed the "Domijean Sands" for widespread outerops on the north flank of Mt. Diablo, Fresno County, California and the type loeality is in the NE¼ of seetion 17, north of Coalinga. The mollusean faunas were described by Clark and Vokes (1936) and Vokes (1939). These faunas became the basis of the "Domengine" [CPMS] of Clark and Vokes (1936), whieh they believed to be middle Eocene (Squires (1988). Most reeently, based on ealeareous nannoplankton and magnetic stratigraphy, Prothero (2001) eonsidered the formation to be early to middle Eocene age.

Bateque Formation

The Bateque Formation of Mina (1956, 1957) was named for outerops along the Paeific side of Baja California, Mexico, from the north end and east side of Laguna San Ignacio to the San Juanieo area about 105 km to the south (Squires and Demetrion, 1992). The formation ranges in age from middle early Eoeene to late middle Eoeene ("Capay" [CPMS] through "Tejon" [CPMS]) based on calcareous nannoplankton, planktonic foraminifers, and mollusks (Squires and Demetrion, 1992).

ABBREVIATIONS

Abbreviations used for institutional catalog and/or loeality numbers, affiliations, and eondensed terminology are as follows (unless indieated otherwise, eolleetions are in California): CIT, California Institute of Teehnology, Pasadena (collections now at LACMIP); CPMS, California provineial molluscan stage; CSUN, California State University, Northridge (collections now at LACMIP); IGM, Instituto de Geología Universidad Naeional Autónoma de Méxieo, Mexico City; LACMIP, Natural History Museum of Los Angeles County, Invertebrate Paleontology Seetion; LACMVP, Natural History Museum of Los Angeles County, Vertebrate Paleontology Seetion; UCLA, University of California, Los Angeles (eollections now at LACMIP); UCMP, University of California, Museum of Paleontology, Berkeley; USGS, United States Geologieal Survey, Menlo Park.

Measurement parameters are defined as follows: length = greatest distance between anterior and posterior ends; width = greatest distanee between lateral margins; and height = greatest distanee between base and dorsum.

SYSTEMATIC PALEONTOLOGY

The classification used here for Cypraeidae follows that of Schilder and Schilder (1971) and Fehse (2001) for Eocypraeidae.

Superfamily Cypraeoidea Rafinesque, 1815
Family Cypraeidae Rafinesque, 1815
Subfamily Bernayinae Schilder, 1927
Tribe Bernayini Schilder, 1927

Genus *Bernaya* Jousseaume, 1884

Type Species: *Cypraea media* Deshayes, 1835, by original designation. Upper middle Eocene (Bartonian Stage), Auvers-sur-Oise, Val-d'Oise (northwest of Paris), France.

Diagnosis: Shell medium to large size; anterior end somewhat carinate; dorsum smooth; spire of medium height and partially covered; aperture wide, sides rounded; anterior and posterior canals deep; fossula smooth, concave, wide.

Remarks: Schilder and Schilder (1971) recognized 22 species and 11 subspecies of worldwide *Bernaya* sensu stricto. Four of their subspecies have been raised to specific status, one species and one subspecies have been reassigned to other genera, three species have been described subsequent to 1971 (see Groves, 1990; 2004), and another new species is described here. This brings the present total to 29 species and six subspecies. Only four of these species are from western North America (Table 1).

Subgenus *Bernaya* Jousseaume, 1884

Bernaya (Bernaya) squiresi new species
(Figures 1–2)

B. (B.) n. sp. Groves, 1997: 7.

Diagnosis: *Bernaya* of large size, anterior and posterior canals deep, spire of medium height, fossula concave and smooth (although columellar dentition extends slightly onto fossula), posterior terminal ridges extend to margins.

Description: Shell of medium to large size, constricted anteriorly; maximum height of shell nearly centered; maximum width of shell slightly posterior of center; aperture wide, straight; dentition coarse to medium; columellar lip with 25 teeth, labral lip with 24 teeth; prominent anterior terminal ridges that form a slight marginal callus.

Comparison: The new species is unlike any other *Bernaya* from western North America. However, it does resemble *Bernaya obesa* (Deshayes, 1865) from the upper middle Eocene (Bartonian) of the Paris Basin, France, particularly the specimen figured by Cossmann and Pissarro (1911: pl. 32, fig. 162-1). The new species is less inflated, more constricted anteriorly, has a wider less sinuous aperture, and has finer dentition than *B. obesa*. Because the posterior terminal ridges are missing in *B. squiresi*, they cannot be compared; however, the anterior terminal ridges of *B. obesa* are more prominent than those of *B. squiresi*. A specimen identified as *B. (B.) obesa*, figured by Perrilliat and others (2003: 43, figs. 5–6) from the middle Eocene San Juan Formation, central Chiapas, southern Mexico, lacks enough shell material for adequate comparison to the new species.

Discussion: Post-burial crushing has damaged the anterior portion of the aperture and dorso-ventrally distorted the specimen. Generic and subgeneric assignment are based on the wide aperture, deep anterior and posterior canals, and medium-height spire. *Bernaya squiresi* represents the northernmost occurrence of the genus in Cenozoic strata and the only representative of the genus described from Washington.

Material: The new species is represented by a single fairly well preserved specimen that exhibits original shell material on the base and minor amounts of original shell material on the dorsum.

Type Material: Holotype LACMIP 13644, measures 52.7 mm in length, 40.0 mm in width, and 26.3 mm in height.

Type Locality: LACMIP loc. 22341 [*ex* UCLA loc. 2341], southwest end of Discovery Bay, Jefferson County, Washington. Middle lower Eocene ("Capay" [CPMS] = Ypresian Stage), Crescent Formation.

Etymology: This species is named after friend and colleague Richard L. Squires (CSUN Geological Sciences) for his extraordinary contributions to molluscan paleontology.

Family Eocypraeidae Schilder, 1924
Subfamily Eocypraeinae Schilder, 1924
Tribe Eocypraeini Schilder, 1924
Genus *Eocypraea* Cossmann, 1903

Type Species: *Cypraea inflata* Lamarck, 1802, by original designation, middle Eocene (Lutetian/Bartonian stages), Paris Basin, France.

Diagnosis: Inflated-pyriform shell of small to medium size; spire involute; narrow elongate aperture; fossula broad, smooth, concave.

Remarks: Schilder and Schilder (1971) recognized 23 species and nine subspecies of *Eocypraea* sensu stricto. Six of their subspecies have been elevated to specific status, five species have been described subsequent to 1971, and four new species are described here which brings the total to 38 species and three subspecies. Nine of these species are from western North America (Table 1). Schilder (1924) established the subfamily Eocypraeinae for various genera of extinct and living cypraeids and ovulids including *Eocypraea* of Cossmann (1903). Schilder (1932) included *Eocypraea* in the family Amphiperatidae (= Ovulidae), subfamily Cypraediinae, but included fossil and living genera of ovulids

Figures 1–12. Paleogene cypraeoideans. **1–2.** *Bernaya* (*Bernaya*) *squiresi* new species, holotype LACMIP 13644, from LACMIP loc. 23341, 52.7 mm length. **3–4.** *Eocypraea* (*Eocypraea*) *takeosusukii* new species, holotype LACMIP 13645 from LACMIP loc. 7045, 18.8 mm length. **5–6.** *Eocypraea* (*Eocypraea*) *batequensis* new species, holotype IGM 5174 from LACMIP loc. 16951, 9.4 mm length. **7–8.** *Eocypraea* (*Eocypraea*) *crescentensis* new species, holotype LACMIP 13646, from LACMP loc. 16655, 10.9 mm length. **9–10.** *Eocypraea* (*Eocypraea*) *jimgoederti* new species, holotype LACMIP 13647, from LACMIP loc. 41573, 12.7 mm length. **11–12.** *Eocypraea* (*Eocypraea*) sp., cf. *E.* (*E.*) *inflata* (Lamarck, 1802), hypotype UCMP 15815 from UCMP loc. A-1282, 27.1 mm length.

only. In 1971 Schilder and Schilder included the subfamily Eocypraeinae in the family Ovulidae and again included living and fossil genera. Fehse (2001) elevated Eocypraeinae to full family status (Eocypraeidae) but included only extinct genera.

Subgenus *Eocypraea* Cossmann, 1903

Eocypraea (*Eocypraea*) *takeosusukii* new species
(Figures 3–4)

E. (*E.*) n.sp. Groves, 1997: 7

Diagnosis: An *Eocypraea* with inflated shell and slightly s-shaped aperture.

Description: Shell moderately inflated, of medium size, constricted anteriorly; spire completely covered; dorsum highly arched; maximum height nearly center; maximum width nearly center; aperture slightly s-shaped and widens anteriorly, curves sharply toward columella posteriorly; denticulation semi-coarse with smooth interstices; outer lip with 16 teeth, inner lip with 11 teeth; fossula smooth, wide; all surfaces smooth; posterior columella highly inflated; posterior canal deep, anterior canal missing; anterior and posterior basal ridges slight and do not form basal calluses; base rounded.

Comparison: *Eocypraea (E.) takeosusukii* is unlike other eocypraeid in the eastern Pacific and is most similar to *Eocypraea bartlettiana* (Maury, 1912: 86–87, pl. 11, figs. 11–13) from the Paleocene (Thanetian Stage) of Soldado Roek, Trinidad, Trinidad and Tobago. The new species differs from *E. bartlettiana* by the lack of a prominent basal callus, coarser dentition, and more sinuous aperture.

Discussion: Good preservation of the holotype permits unequivocal generic assignment. *Eocypraea (E.) takeosusuki* differs from all other eocypraeids in the Western Hemisphere and is the first eocypraeid described from the "Martinez" Formation.

Material: The new species is represented by a single, moderately well preserved specimen exhibiting original shell material on its base and dorsum but with minor amounts of shell missing from the dorsum. The anterior end of the shell is missing.

Type Material: Holotype LACMIP 13645, measures 18.8 mm in length, 14.4 mm in width, 11.2 mm in height.

Type Locality: LACMIP loc. 7045 (*ex* CIT loc. 1589), East of Lower Lake, Lake County, California, "Martinez" Formation.

Etymology: This species is named in honor of the late Takeo Susuki (*ex* UCLA) for his numerous important contributions to the study of invertebrate paleontology of southern California.

Eocypraea (Eocypraea) batequensis new species
(Figures 5–6)

Eocypraea? sp. Squires and Demetrion, 1992: 31, figs. 77–79.
E. (E.) n. sp.1. Groves, 1997: 8.

Diagnosis: An *Eocypraea* with inflated shell and slightly s-shaped aperture.

Description: Shell moderately inflated, of small size, constricted anteriorly and posteriorly; spire covered; maximum height of dorsum slightly posterior of center; maximum width nearly center; aperture slightly s-shaped; denticulation semi-coarse with smooth interstices; outer lip with 24 teeth, inner lip with 18 teeth; fossula smooth, wide; all surfaces smooth; anterior canal shallow, posterior canal deep; anterior and posterior terminal ridges short; slight basal marginal callus on outer lip; base rounded.

Comparison: The new species is unlike any known species in the eastern Pacific. However it somewhat resembles *Eocypraea inflata* (Lamarck, 1802) from the middle Eocene (Lutetian Stage) of Parnes, Oise Department, Paris Basin, France as illustrated by Cossmann and Pissaro (1911: pl. 32, fig. 162-7) and *E. cotteri* Cox (1930: pl. 19, figs. 8a–8c) from the late Paleocene (Thanetian Stage) of the Samana Range of northwest India. *Eocypraea (E.) batequensis* differs from both mainly by its smaller size but also by it's narrower aperture, finer dentition, and less calloused outer lip.

Discussion: Excellent preservation of the holotype permits unequivocal generic assignment. *Eocypraea (E.) batequensis* differs from all other eocypraeids in the Western Hemisphere and is the first described from Baja California Sur, Mexico.

Material: Represented by a single well preserved internal mold.

Type Material: Holotype IGM 5174, measures 9.4 mm in length, 6.5 mm in width, and 5.1 mm in height.

Type Locality: LACMIP loc. 16951 (= CSUN loc. 1220b), Mesa La Salina, Baja California Sur, Mexico, Bateque Formation.

Etymology: This species is named for the Bateque Formation.

Eocypraea (Eocypraea) crescentensis new species
(Figures 7–8)

E. (E.) n. sp. 2. Groves, 1997: 7 (in part).

Diagnosis: An eocypraeid with inflated shell and slightly s-shaped aperture.

Description: Shell moderately inflated, of small size; constricted anteriorly and slightly produced; spire covered; maximum height slightly posterior of center; maximum width nearly center; aperture wide and very slightly s-shaped; dentieulation coarse with smooth interstices, outer lip with 14 teeth, inner lip with 6 teeth; fossula smooth, wide; dorsal surface exhibits linear pattern which could represent growth lines; anterior and posterior canals shallow; anterior and posterior basal ridges reduced forming a slight collumellar basal callus; slight posterior spiral sulcus present; base rounded.

Comparison: *Eocypraea (E.) crescentensis* n. sp. most closely resembles *E. (E.) jimgoederti* n. sp. (this paper) but has a straighter aperture, a less prominent basal collumellar callus, more produced extremities, and a posterior spiral sulcus.

Discussion: Exeellent preservation of the holotype permits positive generic assignment. *Eocypraea* (*E.*) *crescentensis* differs from all other eocypraeids in the Western Hemisphere and is the first eocypraeid deseribed from the Crescent Formation. The new species represents the northernmost record of the genus in western North America.

Material: The new species is represented by the fairly well preserved holotype specimen that exhibits original shell material and a poorly preserved topotypic internal mold that measures 7.8 mm in length, 5.6 mm in width, and 4.3 mm in height, and three small fragments

Type Material: Holotype LACMIP 13646, measures 10.9 mm in length, 7.6 mm in width, and 6.1 mm in height.

Type Locality: LACMIP loc. 16655 (*ex* CSUN loe. 1563), Larch Mountain, Thurston County, Washington, Crescent Formation.

Etymology: This speeies is named for the Crescent Formation, Washington.

Eocypraea (Eocypraea) jimgoederti new speeies
(Figures 9–10)

E. (*E.*) n.sp. 2. Groves, 1997: 7 (in part).

Diagnosis: An eocypraeid with inflated shell and slightly s-shaped aperture.

Description: Shell slightly inflated, of small size; constricted anteriorly and posteriorly and slightly produced; spire covered; dorsum highly arched; maximum height slightly posterior of center; maximum width nearly centered; aperture wide for size, slightly s-shaped; denticulation eoarse with smooth interstices; outer lip with 14 teeth, inner lip with 12 teeth; fossula smooth and wide; all surfaces roughened by preservation; posterior columella moderately inflated; anterior eanal shallow, posterior eanal deep; anterior terminal ridges prominent, posterior terminal ridges slightly reduced; basal marginal callus moderate on outer lip; base roumded.

Comparison: *Eocypraea* (*E.*) *jimgoederti* new species is different from all other eocypraeids from the eastern Pacific but is somewhat similar to a speeimen of *E.* (*E.*) *dollfusi* (Laubrière, 1881) from the middle Eocene (Lutetian Stage) of Parnes, Oise Department, Paris Basin, France as figured by Cossmann and Pissaro (1911: pl. 33, fig. 162-8). The new species has coarser dentition, straighter aperture, and has a less inflated columellar region than *E.* (*E.*) *dollfusi*.

Discussion: Good preservation of the holotype permits positive generic assignment. *Eocypraea* (*E.*) *jimgoederti* differs from all other eocypraeids in the Western Hemisphere and is the second eocypraeid described from the Crescent Formation.

Material: The new speeies is represented by a single fairly well preserved specimen that exhibits original shell material.

Type Material: Holotype LACMIP 13647, measures 12.7 mm in length, 8.2 mm in width, and 6.9 mm in height.

Type Locality: LACMIP loe. 41573 (*ex* CSUN loc. 1573), Doty Hills, Lewis County, Washington, Crescent Formation.

Etymology: This species is named for colleague Jim Goedert, Gig Harbor, Washington, who eollected the holotype and donated it to LACMIP and for his numerous important contributions to Tertiary molluscan paleontology of Washington.

Eocypraea (Eocypraea) sp., cf. *E. (E.) inflata* (Lamarck, 1802)
(Figures 11–12)

Eocypraea castacensis (Stewart, 1926 [1927]): Vokes, 1939: 26, 154, pl. 20, fig. 14.
Cypraea castacensis Stewart, 1926 [1927]: Ingram, 1942: 103, pl. 8, fig. 6.
Eocypraea (Eocypraea) moumieti Dolin and Dolin, 1983: 36; Groves, 1997: 8.

Remarks: The hypotype of Vokes (1939, pl. 20, fig. 14) [UCMP 15815] most closely resembles *E.* (*E.*) *inflata* (Lamarck, 1802) from middle Eocene strata (Lutetian/Bartonian stages) of France, Belgium, and England. This is particularly evident from the illustrations of Cossmann, 1903 (pl. 9, figs. 18–19) and Cossmann and Pissarro, 1911 (pl. 32, fig. 162-7). It also superficially resembles *E.* (*E.*) *maniobraensis* Squires and Advocate, 1986 from the lower Eocene ("Capay" [CPMS]) Maniobra Formation of Riverside County, California. *Eocypraea* (*E.*) *maniobracnsis* is more elongate, has coarser dentition, has a prominent basal callus, and is significantly larger than *E.* (*E.*) sp. cf. *E.* (*E.*) *inflata*.

Vokes (1939) and Ingram (1942) both misidentified this poorly preserved specimen as *E.* (*E.*) *castacensis* (Stewart, 1926 [1927]). Most specimens of *E.* (*E.*) *castacensis* have a fairly prominent basal eallus and it is less globose than *E.* (*E.*) sp., cf. *E* . (*E.*) *inflata*. Dolin and Dolin (1983) described *E.* (*E.*) *moumieti* from the Gan Basin, Pyrénées Atlantique Deptartment, Francc. They included the hypotype of Vokes (1939) as this new species but did not refigure it. Dolin and Ledon (2002) tentatively reassigned *E.* (*E.*) *moumeti* to the eocypraeid genus *Sulcocypraea*. *Eocypraea* (*E.*) sp. cf. *E.* (*E.*) *inflata* differs from *E.* (*E.*) *moumeti* by its finer dentition and a slightly more inflated columellar region.

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Weaver, C.E. 1937. Tertiary stratigraphy of western Washington and northwestern Oregon. University of Washington Publications in Geology 4: 1–266, pls. 1–15.

APPENDIX 1. LOCALITIES CITED

LACMIP loc. 7045 [ex CIT loc. 1589]. 1200 ft. south of bridge over Herndon Creek on Monticello-Lower Lake Highway, 0.8 mile east of Lower Lake, Lake County, California. Latest early or earliest late Paleocene (Danian/Thanetian stages) "Martinez" Formation (uppermost "unnamed" [CPMS] or lowermost "Martinez" [CPMS]). Coll.: W.P. Popenoe, 12 May 1944.

LACMIP 16655 [ex CSUN 1563]. At elevation of 2230 ft. (680 m), exposed in roadcut on northeast side of logging road, latitude 47°59′3″ N, longitude 123°8′12″ W, 300 m north and 50 m east of southwest corner of sec. 1, T17N, R4W and 500 m S32E of Larch Mountain, U.S. Geological Survey, 7.5 minute, Capital Peak Quadrangle, provisional edition 1986, Black Hills, Thurston County, Washington. Upper part of the Crescent Formation. Age: Middle early Eocene ("Capay" [CPMS]). Coll. J.L. and G.H. Goedert, July, 1992 and September, 1997.

LACMIP 16951 [ex CSUN loc. 1220b]. Along a prominent ridge, north side of a minor canyon on the west side of Mesa La Salina, 84–130 m above the bottom of the Bateque Formation in this area, approximately 1.25 km southeast of the intersection of 113 °00′ W and 26°45′ N, Mexican government topographic quadrangle map (1:50,000) of San José de Gracia (#G12A64), Baja California Sur, Mexico (1982 ed.). Coll.: R.L. Squires and R.A. Demetrion, 1988.

LACMIP 23341 [ex UCLA 3341]. Southwest end of Discovery Bay, on Highway 101, 1000 ft. south of Maynard, sec. 23, T29N, R2W, Jefferson County, Washington. Middle early Eocene (Ypresian Stage), Crescent Formation ("Capay" [CPMS]). Coll.: H.C. Jamison and S.D. Conrad, April, 1952.

LACMIP 41573 [ex CSUN 1573]. In a "borrow pit" 228 m south and 548 m east of northwest corner of sec. 23, T14N, R5W, U.S. Geological Survey, 7.5 minute, Doty Quadrangle, provisional edition 1986, Lewis County, Washington. Crescent Formation. Age: Middle Eocene ("Domengine" [CPMS]). Coll. J.L. Goedert, 1993–1994.

UCMP A-1282. Approximately 100 feet below the uppermost fossiliferous layer, near the center of north edge of section 20, on hill slope immediately south of point where the Big Tar – McClure Rd. crosses saddle at head of stream running into McClure Valley, T23S, R17E, U.S. Geological Survey, 15 minute, Cholame Quadrangle, Kings County, California. Age: Middle Eocene ("Domengine" [CPMS]).

Descriptions and illustrations of some new and poorly known turrids (Gastropoda: Turridae) of the tropical northwestern Atlantic. Part 3. Genus *Crassispira* Swainson, 1840, subgenus *Crassisclava* McLean, 1971

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ABSTRACT

Illustrations and descriptions of eight small turrids in the genus *Crassispira* Swainson, 1840, subgenus *Crassiclava* McLean, 1971, are provided. Five are described for the first time. All are from shallow water around islands of the southeastern Caribbean (between 10°–13° north latitude) and appear to represent an example of divergenee among isolated island populations in a small geographie region. Species include *Crassispira* (*Crassiclava*) *affinis* (Reeve, 1846), *Crassispira* (*Crassiclava*) *asthenes* Faber, 2007, *Crassispira* (*Crassiclava*) *blanquilla* new species, *Crassispira* (*Crassiclava*) *cana* new speeies, *Crassispira* (*Crassiclava*) *mackintoshi* new species, *Crassispira* (*Crassiclava*) *masinoi* new species, *Crassispira* (*Crassiclava*) *multicostata* new species, and *Crassispira* (*Crassiclava*) *vexillum* (Reeve, 1845). Speeies are treated systematieally and the island or island groups where they have been found illustrated to emphasize their very limited distributions and geographie proximity. The five reported here for the first time represent a sizeable range expansion of the known subgenus-group *Crassiclava* in the western Atlantie; and inasmuch as several islands along the north coast of South America have yet to be explored, additional species of *Crassiclava* may turn up.

Additional keywords: Neogastropoda, western Atlantic

INTRODUCTION

This is the third in a series of papers describing small relatively unknown or confusing erassispirine turrids. In this part, eight species in the subgenus *Crassiclava* McLean, 1971 are discussed, five new to seienee.

Reeently, some heretofore undescribed crassispirines have been acquired from a rather small geographic region of the southeastern Caribbean, islands and areas near coastal South Ameriea that lie between 10°–13° N (Figure 1). Their elose resemblance to one another and to known members of the subgenus suggests a close evolutionary affinity; most apparently limited in distribution to a single island or island elusters with no known overlap. Such diversity in *Crassiclava* has likely been fostered by the isolation of small populations that have direct developing non-planktonic larvae, and a habitat preference for the shallow water aromnd islands separated from one another by deep water, likely a barrier to dispersal. The mode of development is only inferred here; however, Maes (1983: 322) states that the protoconeh of a speeies in the same subgenus, *Crassispira* (*Crassiclava*) *apicata* (Reeve, 1845), suggests full intracapsular development.

The purpose of this work is to deseribe five previously undescribed species that belong in the subgenus-group *Crassiclava* MeLean, 1971, to re-describe *Crassispira* (*Crassiclava*) *affinis* (Reeve, 1846), a little-known and misunderstood species, on the basis of specimens found that closely match Reeve's description (the type has not been located), and to re-describe *Crassispira* (*Crassiclava*) *vexillum* (Reeve, 1845) to provide a basis by which it ean be compared to the other members of the subgenus. Another, *Crassispira* (*Crassiclava*) *asthenes* Faber, 2007, has beeu included for comparison purposes but its original description is sufficiently detailed and so not re-deseribed here.

MATERIALS AND METHODS

Materials and methods given in Part 1 of this series (Fallon, 2010), apply to this work. Since that publication, types located at the Natural History Museum (London) (NHMUK) have been examined and photographed for this work, in addition to specimens in the collections of the National Museum of Natural History (USNM) and Academy of Natural Sciences of Philadelphia (ANSP). St. Vincent and the Grenadines is abbreviated SVG herein.

SYSTEMATICS

Subfamily Crassispirinae Morrison, 1966, *sensu* McLean, 1971a, b

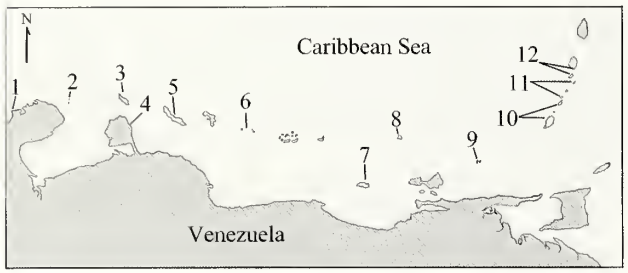


Figure 1. Southern Caribbean *Crassispira (Crassiclava)* spp. localities. 1. Cabo de la Vela. 2. Los Monjes Is. 3. Aruba I. 4. El Supi, Paraguaná Peninsula. 5. Curaçao I. 6. Las Aves Archipellago. 7. La Tortuga I. 8. La Blanquilla I. 9. Los Tostigos Is. 10. Carriacou I., Ronde I., and Grenada I., Grenada, north to south. 11. Petit Nevis I., Baliceaux I., Canouan I., and Union I., SVG, north to south. 12. St. Vincent I., Young I. and Bequia I., north to south, SVG (not all appear on map).

Genus *Crassispira* Swainson, 1840
Subgenus *Crassiclava* McLean, 1971

Type Species: *Pleurotoma turricula* G.B. Sowerby I, 1834 (synonyms: *P. corrugata* G.B. Sowerby I, 1834; *P. sowerbyi* Reeve, 1843), by original designation. Santa Elena, "western Colombia" (no coastal locality by that name is found in present day Colombia.)

Remarks: McLean placed two species from the west coast [eastern Pacific] in his new subgenus describing them as having a protoconch of 2.5 smooth rounded whorls; strong narrow axial ribs that arise at the whorl periphery, and extend to the following suture; fine spiral cords, strongest anteriorly where they are slightly nodulose at rib intersections; weakly nodded subsutural cord; concave sulcus; thin outer lip, edge crenulated by spiral cords; shallow stromboid notch; deep U-shaped anal sinus, broad at its entrance, bordered by a large parietal callus; varix consisting of a thickened axial rib behind the anal sinus; inner lip raised; and a broad, deeply notched anterior canal. Furthermore, he identified two characters that separated this group from other eastern Pacific crassispirines: a strong parietal tubercle in front of a broad sinus entrance, and a radula with a well-formed central rachidian tooth and marginal teeth of modified wishbone or duplex type (McLean, 1971: 121). Later, Maes corrected McLean's analysis of the radula, finding his central tooth was really two unhardened lateral teeth such that the radula of the subgenus has no central tooth (Maes, 1983: 321).

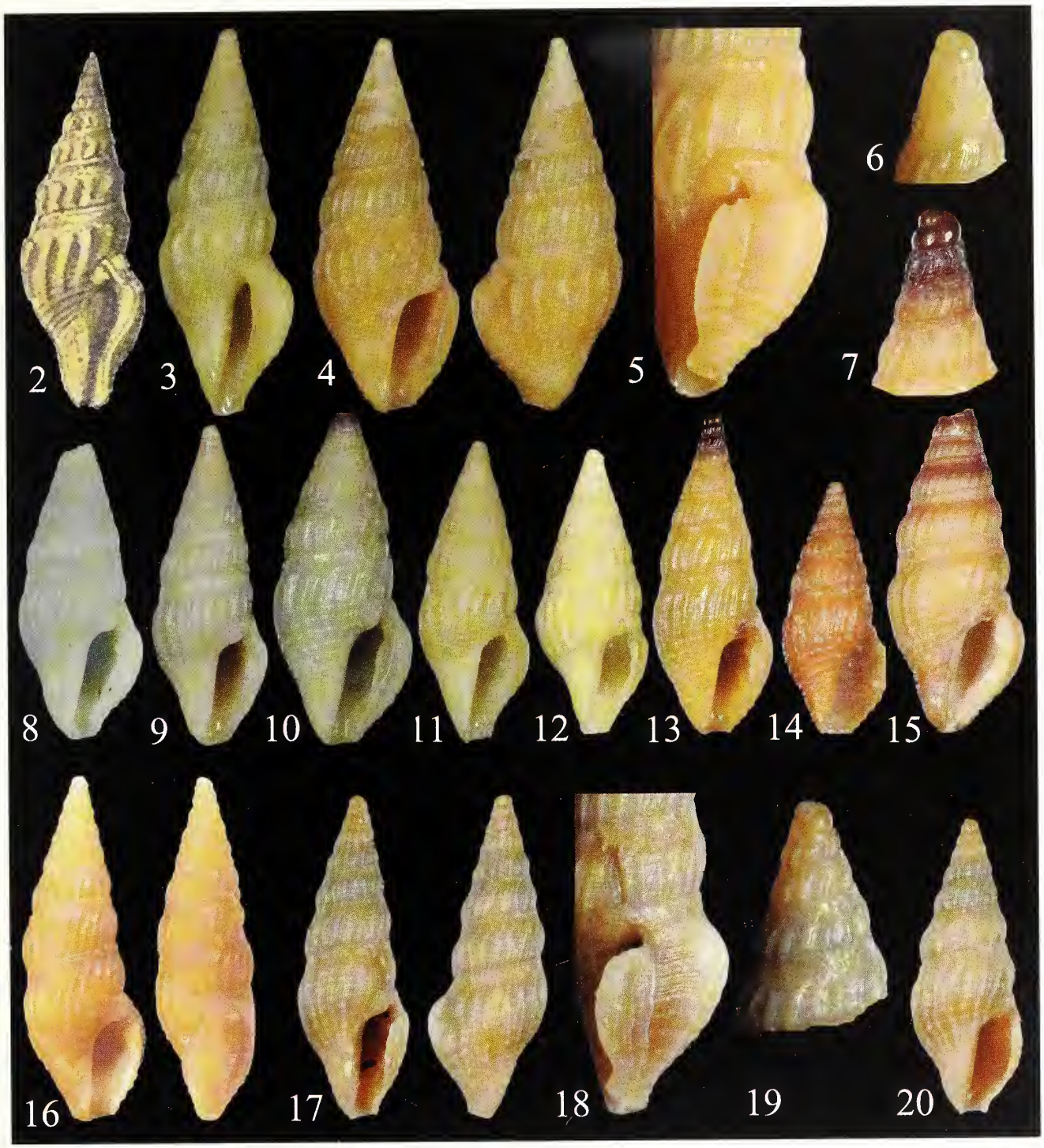
Although McLean believed that his group was confined to the tropical western Pacific, Maes recognized the radula of a tropical northwestern Atlantic (TNWA) species she identified as *Crassispira (Crassiclava) apicata* (Reeve, 1845) as very similar to that of *Crassispira (Crassiclava) turricula* (G.B. Sowerby I, 1834), the type of the subgenus (Maes, 1983: 322). The sculptural details of her specimens from the British Virgin Islands (Maes, 1983: fig. 15) differ somewhat in that axial ribs are weak, not strong, and extend well into the sulcus, not ending at it. Kilburn soon afterwards added four species to *Crassiclava* from the South African fauna (Kilburn, 1988: 239). His descriptions varied slightly from McLean's original, in that the subsutural cord was absent to moderately strong, and the siphonal canal varies from unnotched to deeply notched in South African species.

In summary, members of the subgenus *Crassiclava* of the TNWA have shell characters consistent with those described by previous workers. They are crassispirines having: a strong parietal lobe in front of an open, U-shaped anal sinus; a weakly to moderately excavated sulcus without, or with spiral threads, some more swollen than others, or with a weak spiral cord; fine axial ribs that extend from the suture to the shell base, usually reduced and narrowed in the sulcus; spiral threads or incised lines in rib interstices; and widely spaced cords or ridges on the shell base, sometimes swollen or nodulose at rib intersections.

Crassispira (Crassiclava) affinis (Reeve, 1846)
(Figures 2–15)

Pleurotoma affinis Reeve, 1846: pl. 34, fig. 309 (name attributed to Gray). The type could not be located; however, the coloration ("yellowish"), extrapolated size (11.8 mm), and locality ("St. Vincent") of Reeve's species are consistent with the specimens described here (see comparison in Figures 2, 3). Beau (1858: 8); Krebs (1864: 7); Paetel (1888).
Mangelia affinis "Gray": H. & A. Adams (1853: 99).
Drillia affinis "Gray": Tryon (1884: 194; pl. 21, fig. 22).
Pleurotoma affinis "Gray": Dall (1885: 232).
Crassispira apicata auct. non (Reeve, 1845): misidentification by Fallon (2008: 12, figs. 21a–c).
Not *Crassispira (Crassispirella) affinis* (Reeve, 1846): Altena (1975: 63, pl. 7, figs. 5, 6).
Not *Crassispira affinis* (Reeve, 1846): Williams (2005: number 3130, except the inset in the left photo, which is Reeve's drawing); Faber (2007: 123, figs 10, 11, 18).

Description: A 12.3 × 5.0 mm specimen is described here (Figures 4–5) (length to 12.9 mm). Fusiform, truncated anteriorly, of 9 convex whorls; apex slightly acuminate; axial sculpture predominant. Suture appressed; sulcus about 0.3 height of spire whorl, moderately excavated; shoulder round, or slightly angled in some specimens. Body whorl 61% of total shell length (56–62 % among intact specimens). Protoconch paucispiral, of 2 smooth slightly worn whorls, obscuring axial riblets, if present (Figure 6); 10.5 mm Baliceaux I. specimen has 10 riblets on last 0.5 whorl of protoconch (Figures 7). Axial sculpture of narrow, low, slightly opisthocline ribs, reduced in sulcus to mere raised lines that are hooked to left in an arc that reflects outline of anal sinus, thickest just below sulcus, tapering anteriorly, evanescing on shell base; 26 ribs on penultimate, 14 on last whorl (15–26 on penultimate, 11–22 on last whorl of examined specimens); ribs generally narrower than interspaces, variable, sometimes broad, indistinct, especially on body whorl. Growth striae present; visible in sulcus. Spiral sculpture of numerous spiral threads in sulcus, one or



Figures 2–20. *Crassispira* spp. **2–15.** *Crassispira* (*Crassiclava*) *affinis* (Reeve, 1846). **2.** *Pleurotoma affinis* Reeve, 1846. Drawing from Reeve, 1846: 34, fig. 309, 11.8 mm. **3.** USNM 1154261, Carriacou I., Grenada, 12.9 × 4.5 mm. **4.** BMSM 17955, Ronde I. Grenada, 12.4 × 5.0 mm. **5.** Same spec. as in 4, enlarged view of anterior lateral side. **6.** Protoconch, author's coll., Union I., SVG, 8.0 × 3.1 mm. **7.** Protoconch, ANSP 425811, Baliceaux I. SVG, 10.5 × 4.0 mm. **8.** Author's coll., Devil's Bay, Grenada, 9.8 × 4.2 mm. **9.** FLMNH 446785, Union I., SVG, 10.6 × 3.7 mm. **10.** Author's coll., Canouan I., SVG, 11.5 × 4.6 mm. **11.** Author's coll., Union I., SVG, 10.0 × 3.5 mm. **12.** Author's coll., Union I., SVG, 9.4 × 3.7 mm. **13.** ANSP 425811, Baliceaux I. SVG, 10.5 × 4.0 mm. **14.** Author's coll., Union I., SVG, 8.3 × 3.6 mm. **15.** BMSM 17954, Petit Nevis I., SVG, 10.7 × 4.5 mm. **16.** *Crassispira* (*Crassiclava*) *asthenes* Faber, 2007. Holotype, ZMA Moll. 4.07.057, Aruba, 11.4 × 4.2 mm (photograph courtesy Marien Faber). **17–20.** *Crassispira* (*Crassiclava*) *masinoi* new species. **17.** Holotype, USNM 1154263, off Santa Martha Beach, Curaçao I., 10.7 × 3.8 mm. **18.** Holotype, enlargement of anterior lateral view. **19.** Paratype, ANSP 425814, type locality, 9.8 × 3.8 mm. **20.** Same spec. as in 19, enlarged view of protoconch.

more swollen; fine spiral grooves present on shell face overriding axial ribs; flattened cords on shell base that are slightly nodulose at intersection with axial ribs, nodules becoming more pronounced anteriorly. Seven (5–8) spiral ridges on anterior fasciole. Outer lip thin, projects a short distance out from base of varix, strengthened behind by short axial; shallow stromboid notch present (Figure 5). Varix, moderately large, angled at shoulder, appearing hump-like, positioned behind anal sinus. Anal sinus deep, round at its apex, bordered by parietal lobe on one side. Two low spiral ridges present on inside of outer lip (0–2 ridges in other specimens) strongest just below anal sinus underneath varix, its length same as width of varix; the other less well defined and broader, lies near stromboid notch and marks beginning of siphonal canal. Inner lip appressed along entire length; thickened anteriorly, very thin on parietal wall. Aperture narrowly oval and ends anteriorly in short unnotched siphonal canal. Shell color yellow-orange; specimens may also be light brown, orange-brown, yellow, and very pale lemon yellow. May or may not have brown spire tip. A sampling of color forms appears in Figures 8–15.

Type Material: Not located.

Material Examined: A total of 131 specimens from 12 localities have been examined:

1 spec., 11.8 × 4.6 mm, at 12 m, Petit Nevis I., SVG, G. Mackintosh!, 13 May 1993 (USNM 1154259); 2 spec., 10.7 × 4.5 (Figure 15) and 10.1 × 4.2 mm (both decollate), at 7.6 m, Petit Nevis I., SVG, G. Mackintosh! 16 May 1993 (BMSM 17954); 1 spec., 10.3 × 3.8 mm, at 7.6 m, Petit Nevis, SVG, G. Mackintosh! 14 Jul 1996 (author's coll.); 2 spec., 10.5 × 4.0 (Figures 7, 13) and 9.6 × 3.8 mm, at 12.2 m, S end of Baliceaux I., SVG, G. Mackintosh!, 23 Apr 1997 (ANSP 425811); 6 spec., 10.2 × 3.8, 10.2 × 4.1, 9.2 × 3.8, 10.8 × 4.0, 9.6 × 3.3, and 11.4 × 4.2 mm, at 4.6–7.6 m, Corbay Bay, Canouan I., SVG, G. Mackintosh! 6–9 June 2004 (USNM 1154260); 1 spec., 11.5 × 4.6 mm (Figure 10), at 4.6 m, Dove Cay, Canouan I., SVG, G. Mackintosh! 6 June 2004 (author's coll.); 21 spec., largest 10.8 × 4.0, smallest 7.4 × 3.1 mm, at 5.5 m, Corbay Bay, Canouan I., SVG, G. Mackintosh! 6 Dec 2006 (author's coll.); 2 spec., 11.3 × 4.2 and 9.4 × 3.7 mm (Figure 12), at 20 m, 0.4 km E of "Bloody Head", NW Union I., SVG, R. Masino! 31 Aug 2010 (author's coll.); 22 spec., largest 11.6 × 4.4, 10.0 × 3.5 (Figure 11), and smallest 7.9 × 3.2 mm, at 18 m, Chatham Bay, Union I., SVG, G. Mackintosh! 6 Apr 2007 (author's coll.); 5 spec., 10.7 × 3.8, 8.8 × 3.4, 8.9 × 3.3, 7.8 × 2.9, and 8.1 × 2.9 mm, at 9 m, Clifton Harbor, Union I., SVG, G. Mackintosh! 10 May 2007 (ANSP 425810; 8 spec., 10.6 × 3.7 (Figure 9), 10.2 × 3.6, 11.1 × 3.9, 10.1 × 3.7, 8.6 × 3.3, 8.3 × 3.0, 8.0 × 3.3, and 7.6 × 2.7 mm, at 11 m, Clifton Harbor, Union I., SVG, G. Mackintosh! 30 May 2004 (FLMNH 446785); 56 spec., intertidal, crabbed and worn, up to 10.6 × 4.5 mm, broken apex, 8.3 × 3.6 mm specimen in Figure 14, Clifton Harbor, Union I., SVG, P. Fallon!, 16 Jun 2007 (author's coll.); 1 spec., 12.9 × 4.5 mm (Figure 3), at 9 m. NW coast, Carriacou I., Grenada, G. Mackintosh! Dec 1996 (USNM 1154261); 1 spec., 10.9 × 4.2 mm, at 15 m, SE corner, Ronde I., Grenada, G. Mackintosh! 25 Jan 1997 (author's coll.); 1 spec., 12.3 × 5.0 mm (Figures 4, 5), at 6.7 m, Ronde I., Grenada (BMSM 17955); 2 spec., 12.2 × 5.3 (broken tip) and 10.7 × 3.8 mm (immature lip), at 4.6 m, Ronde I., Grenada, G. Mackintosh! 30 Dec 2006 (ANSP 425812); 1 spec., 8.9 × 3.6 mm, at 6.7 m, S side of Molinere Pt., Grenada, G. Mackintosh!, 18 Apr 2004 (author's coll.); 2 spec., 10.7 × 4.1 and 8.7 × 3.4 mm, at 6.7 m, outside anchorage, St. Georges, Grenada, G. Mackintosh!, 24 Jun 2003 (USNM 1154262); 2 spec., 8.6 × 3.7 and 9.8 × 4.2 mm (Figure 8), both decollate, at 9 m, Devil's Bay, Grenada (author's coll.).

Type Locality: "St. Vincent".

Range: St. Vincent and the Grenadines (Petit Nevis I., Baliceaux I., Canouan I., Union I.) and Grenada (Carriacou I., Ronde I., Grenada I.) (locations "10" and "11" in Figure 1).

Remarks: The similarity of Reeve's drawing (which is taken as representative of the type) to the specimens here identified as *Crassispira affinis* is illustrated by the juxtaposition of the drawing of *Pleurotoma affinis* (Reeve's pl. 34, fig. 309) with a 12.9 × 4.5 mm specimen from Carriacou I., Grenada, in Figures 2 and 3. The drawing and selected specimen are very similar but there are some small differences that may be due to "artistic license". Axial ribs appear to end at the sulcus in the drawing, whereas they continue into the suture in specimens in hand, albeit much reduced. The anterior end of Reeve's drawing appears to be somewhat narrower, a feature characteristic of less mature shells. While the type of *C. affinis* would have been examined for subtle characters not shown in the drawing, the likelihood of a very similar but different species inhabiting the environs of St. Vincent and the Grenadines with the observed degree of similarity is remote, especially given the commonness of these specimens.

C. affinis is most easily recognized by its yellow or yellowish colors, which is unique among the *Crassiclava*. From *Crassispira* (*Crassiclava*) *asthenes* Faber, 2007 (Figure 16) it differs in having less regular axial ribs and a longer anterior canal. *Crassispira asthenes* is described as uniformly light brown in color (Faber, 2007: 123), not the yellow of *C. affinis* (the color of the specimen shown in Figure 16 is off).

Crassispira (*Crassiclava*) *masinoi* new species
(Figures 17–20)

Description: Holotype 10.7 × 3.8 mm, fusiform, truncated anteriorly, of 8.5 convex whorls; body whorl 56% of total shell length (paratype 57%). Suture appressed; sulcus moderately excavated, about 0.3 whorl high; shoulder round; axial sculpture predominant (Figures 17, 18).

Protoconch paucispiral, of 1.5 smooth whorls with 3 faint riblets at end (Figure 19). Axial sculpture of slightly opisthoclinc ribs, narrower than their interspaces, with occasionally 2 or 3 ribs bunched together on last whorl. Ribs reduced and hooked to left in sulcus, thickest just below sulcus, and extending to anterior fasciole; 21 ribs on penultimate, 14 on last whorl. Spiral sculpture of grooves of varying strengths on whorl face, fainter on axial rib crests, deeper in interspaces; more widely spaced and deeper on shell base such that axial ribs appear slightly nodulose. Sulcus without spiral cord; with microscopic spiral lines and growth striae in addition to axial ribs. Six spiral cords on anterior fasciole. Outer lip thin, edge smooth, strengthened behind by 3 short axial ribs; shallow stromboid notch present (Figure 18). Varix narrower at shoulder but abruptly broadens immediately below; positioned about 0.25 whorl before edge of outer lip. Anal sinus deep, round at its apex, open at lip edge. Inner lip appressed along its entire length, thicker anteriorly, thin in parietal area, and ending with large round parietal lobe posteriorly. Edge of lip and parietal lobe visibly layered. Low spiral ridge present inside inner lip just anterior to sinus and under varix, its length limited to width of varix. Aperture narrowly oval and ends anteriorly in short, open siphonal canal. Shell honey-colored; rib crests, mid-whorl band, and shoulder of varix whitish.

Type Material: Holotype: USNM 1154263. Paratype: 1 spec., 9.8 × 3.8 mm, type locality (ANSP 425814) (Figure 20).

Type Locality: 0.4 km WNW off Santa Martha Beach, 0.8 km W of Santa Martha Bay entrance, W coast, Curaçao I., Netherlands Antilles, at 34 m depth.

Range: Known only from the type locality (location "5" in Figure 1).

Remarks: *Crassispira masinoi* is a distinctive species recognizable by its honey-colored base color, whitish mid-whorl band and varix, lack of subsutural cord, and its single, paired, or triple axial ribs. It is closest in appearance to *C. asthenes* but that species has a different varix and possesses a subsutural cord. From *C. affinis* it differs in possessing axial ribs that extend to the anterior fasciole. Differences from other *Crassiclava* follow under their descriptions below.

Etymology: Robert Masino's *Crassiclava*. Named for Mr. Robert Masino of Ft. Myers, Florida who collected the type specimens.

Crassispira (*Crassiclava*) *blanquilla* new species
(Figures 21–26)

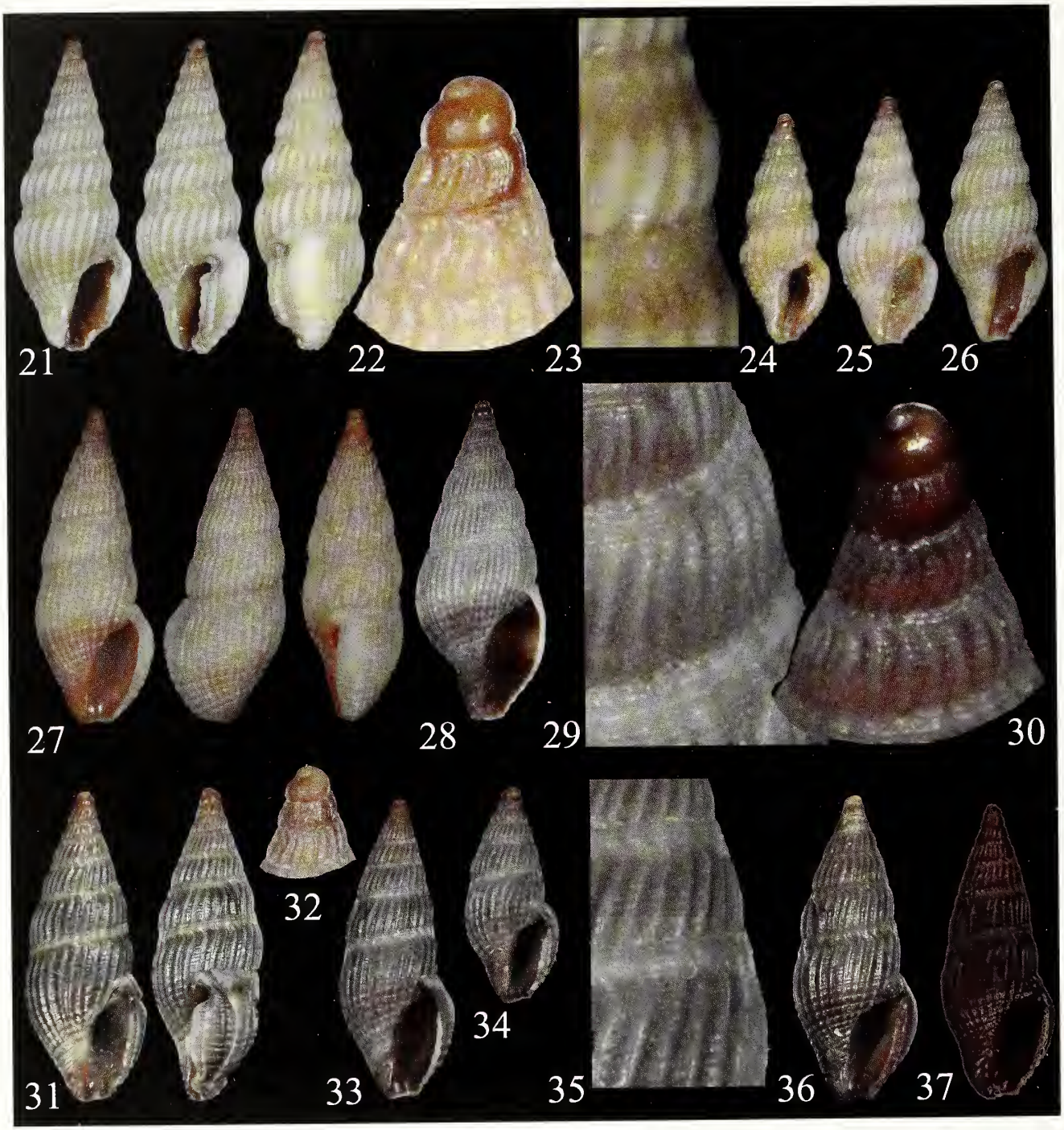
Description: Holotype 10.2 × 3.9 mm (lengths to 10.3 mm), fusiform, truncated anteriorly; of 9 moderately convex whorls; axial sculpture is predominant. Suture appressed, scalloped by ribs; sulcus height approximately 0.3 whorl, moderately excavated. Body whorl 52% of shell length (52–60%) (Figure 21). Protoconch paucispiral, of 2 smooth whorls, last 0.5 whorl with weak axials (Figure 22). Axial sculpture of narrow almost thread-like ribs, 25 on penultimate whorl, 20 on body whorl to varix (22–25 on penultimate, 15–20 on body whorl to varix of type specimens), narrower than interspaces, slightly opisthocline, extending from near suture to following suture, evanescing on shell base. Ribs in sulcus are curved to left reflecting outline of anal sinus, reduced in thickness and height, and terminate in slight swelling near suture in some specimens. Spiral sculpture of closely packed spiral threads in sulcus, 2 closest to suture swollen, flattened, override swollen ends of axial ribs (Figure 23); incised spiral lines cover remaining shell, faint or obsolete on rib crests, deeper in interspaces. Five spiral grooves on shell base cut axial ribs into low squarish nodules, a few shallower spiral incised lines lie in-between ridges. 5 or 6 spiral cords run along anterior fasciole. Outer lip thin and smooth, projecting out a short distance from a thickened varix, strengthened by an axial rib between varix and edge of lip. Varix broad, positioned behind anal sinus. Stromboid notch shallow, marking transition of aperture to short, open anterior canal, unnotched. Anal sinus deep, U-shaped, bordered on one side by heavy parietal lobe. Low spiral ridge present inside inner lip just anterior to sinus and under varix, its length limited to width of varix. Inner lip is narrow, thick anteriorly, very thin on parietal wall and terminating in parietal lobe where outer lip joins. Shell color creamy white, rib crests paler, apex light brown; shell base and sulcus of holotype with diffuse bands of light brown; yellow or orange-yellow bands on some paratypes. Aperture color corresponds to specimens' band color—brown, dark yellow or dark orange-yellow.

Type Material: Holotype: (USNM 1154264). Paratypes: 1 spec., 10.3 × 3.9 mm (missing protoconch), at 18.3 m, La Blanquilla I., Venezuela, G. Mackintosh!, 1 Jan 2000 (USNM 1154265); 2 spec., 6.2 × 2.8 and 7.3 × 2.8 mm, at 7.6 m, La Blanquilla I., Venezuela, G. Mackintosh!, 4 Jan 2000 (ANSP 425813); 2 spec., 7.6 × 3.1 (Figure 24) and 7.5 × 3.0 mm, at 7.6 m, La Blanquilla I., Venezuela, G. Mackintosh!, 4 Jan 2000 (FLMNH 446786); 2 spec. 8.1 × 3.3 (Figure 25) and 8.6 × 3.5 mm (Figures 23, 26), at 7.6 m, La Blanquilla I., Venezuela, G. Mackintosh!, 4 Jan 2000 (author's coll.).

Type Locality: La Blanquilla Island, Venezuela, in 7.6–18 m depths.

Range: Known only from the type locality (location "8" in Figure 1).

Remarks: *Crassispira blanquilla* differs from *C. affinis* in having more uniformly spaced axials ribs, and in possessing a darker colored aperture. From *C. asthenes* it differs in having a more pinched shell base, and different coloration; *C. asthenes* is uniformly light brown with the protoconch paler whereas *C. blanquilla* is creamy white, with a brown protoconch. From *C. masinoi* it



Figures 21–37. *Crassispira* spp. **21–26.** *Crassispira* (*Crassiclava*) *blanquilla* new species, all from type locality. **21.** Holotype, USNM 1154264, 10.2 × 3.9 mm. **22.** Holotype, enlarged view of protoconch. **23.** Paratype, Author's coll., 8.6 × 3.5 mm, enlarged view showing sulcus. **24.** Paratype, FLMNH 446786, 7.6 × 3.1 mm. **25.** Paratype, author's coll., 8.1 × 3.3 mm. **26.** Paratype, author's coll., type locality, 8.6 × 3.5 mm. **27–30.** *Crassispira* (*Crassiclava*) *multicostata*, new species, all from off El Supi, Paraguaná Peninsula, Venezuela. **27.** Holotype, USNM 1154266, 11.0 × 4.3 mm. **28.** Paratype, USNM 1154267, 10.4 × 4.1 mm. **29.** Enlarged view of sulcus of paratype. **30.** Enlarged view of protoconch of paratype. **31–37.** *Crassispira* (*Crassiclava*) *mackintoshi* new species. **31.** Holotype, USNM 1154268, Los Testigos Is., Venezuela, 10.2 × 3.9 mm. **32.** Holotype, enlarged view of protoconch. **33.** Paratype, ANSP 425815, type locality, 9.8 × 3.7 mm. **34.** Paratype, BMSM 17953, type locality, 7.0 × 3.0 mm. **35.** Enlarged view of sulcus, spec. in Figure 33. **36.** Author's coll., Cabo de La Vela, La Guajira Prov., Colombia, 9.9 × 4.0 mm. **37.** Specimen from off Los Monges Is., Venezuela, 9.6 mm (photograph courtesy Femorale).

differs in having more uniformly spaced axial ribs, spiral threads in the sulcus, and a shorter anterior canal. It also differs in coloration.

Etymology: Named after the type locality, La Blanquilla Island, Venezuela. Name in apposition.

Crassispira (*Crassiclava*) *multicostata* new species
(Figures 27–30)

Description: Holotype 11.0 × 4.3 mm, fusiform, anteriorly truncated, of 8.75 moderately convex whorls; axial sculpture is predominant (Figure 27). Suture appressed; sulcus, slightly excavated, narrow, width approximately 0.25 whorl height; shoulders round. Body whorl 55% of shell length (paratype 59%). Protoconch worn on holotype; of 2 glassy whorls with 8 riblets on last 0.5 whorl of paratype (Figure 30). Axial sculpture of fine, almost thread-like, slightly opisthocline ribs that extend to anterior fasciole on body whorl. Ribs slightly reduced and hooked to the left in sulcus, rib ends swollen near suture; microscopic growth striae between axial ribs. Distance between ribs variable; average about the same as their width; 35 ribs on penultimate, 30 on last whorl. Spiral sculpture of up to 5 threads in sulcus of last whorl (Figure 29), fewer in earlier whorls; spiral threads override axial ribs; no subsutural cord present. Shallow spiral grooves cover remaining portion of whorls, more widely spaced on shell base. Rib segments between spiral grooves slightly swollen, more so and forming 7 slightly nodulose rows on shell base. Seven smooth spiral cords on anterior fasciole. Outer lip chipped on holotype, so no visible stromboid notch; varix broad, about 4–5 axial ribs in width, and immediately precedes anal sinus. Anal sinus shallow, incompletely formed, paratype has thin, straight lip, sinus not yet formed. Inner lip narrow, thin and appressed to columella; weak parietal callus present where outer lip joins. Anterior canal very short, open, unnotched. Color creamy white, axial ribs white, broad orange band on shell base, spire apex and aperture dark orange. Paratype is purple-brown, axial ribs white, apex and aperture brown.

Type Material: Holotype: USNM 1154266; paratype: 10.4 × 4.1 mm (Figure 28), from type locality (USNM 1154267) (A. Jorio and L. Couto!).

Type Locality: Off El Supi, Paraguaná Peninsula, Falcón, Venezuela, in 33 m depth.

Range: Known only from the type locality (location "4" in Figure 1).

Remarks: *Crassispira multicostata* is easily distinguished from other *Crassiclava* by its greater number of axial ribs. From *C. affinis* it differs in having a shorter anterior canal, and thinner, more and better defined ribs, and in coloration. From *C. asthenes* it also differs in coloration (*C. asthenes* is uniformly light brown). From *C. masinoi* it also differs in having a narrower sulcus and in possessing spiral threads in the sulcus. Its coloration is similar to *C. blanquilla*, but it differs in having slightly less convex whorls and a narrower sulcus.

Etymology: The Many-ribbed *Crassiclava*. From Latin *multi*—many and *costata*—ribbed. This species has more axial ribs than any other known *Crassiclava*.

Crassispira (*Crassiclava*) *mackintoshi* new species
(Figures 31–36)

Description: Holotype 10.2 × 3.9 mm (lengths to 12.4 mm), compact-oval shape, of 8.5 convex whorls total. Suture appressed; sulcus narrow, only slightly excavated, approximately 0.25 whorl in height; shoulder round, whorls slightly convex. Body whorl 54.9% of shell length (55–65% in examined specimens) (Figure 31). Protoconch paucispiral, of 1.75 whorls; last 0.5 whorl with 6 weak axials, the first few weakest, visible only on whorl's shoulder (Figure 32). Teleoconch of 6.25 whorls; axial sculpture is predominant. Axial sculpture of narrow, slightly opisthocline ribs narrower than interspaces, extending from suture to suture, slightly swollen at their ends near the suture, curved or hooked left in sulcus, reflecting outline of anal sinus and reduced in thickness and height; evanescing on base of shell. Ribs number 30 on penultimate, 27 on last whorl (range is 24–31 on penultimate, 18–30 on last whorl). Spiral sculpture of closely packed threads in sulcus, those near suture swollen (Figure 35); incised spiral lines on whorl face, faint on rib crests but distinct in interspaces; of 6 spiral cords on shell base that cut axials into squarish, low nodules at intersection with axial ribs; 7 spiral cords on anterior fasciole. Outer lip thin, smooth, projects out a short distance from varix, which is positioned behind anal sinus, strengthened by a rib; low spiral ridge present on inside of outer lip just below anal sinus. Anal sinus deep, U-shaped, bordered on one side by heavy parietal lobe. Stromboid notch marks transition of aperture to short, open anterior canal. Inner lip is narrow, appressed to columella, thick anteriorly, very thin on parietal wall. Base color dark gray; shell apex, columella, and tip of anterior canal brown; very light gray to white band present below suture; crests of axial ribs and spiral cords on anterior canal white. An all-brown form exists.

Type Material: Holotype: USNM 1154268. Paratypes, all from the type locality: 2 spec., 9.8 × 3.7 (Figure 33, 35) and 6.8 × 3.0 mm (ANSP 425815); 2 spec., 9.3 × 3.5 and 6.9 × 3.0 mm, missing protoconch (FLMNH 446787); 2 spec., 7.0 × 3.0 (Figure 34) and 7.5 × 3.0 mm, broken protoconch (BMSM 17953); 2 spec., 8.8 × 3.6 and 8.1 × 3.6 mm, broken spire (P. Williams coll.).

Type Locality: North of Testigos Grande, Los Testigos Islands, Venezuela, at 6.1 m depth (G. Mackintosh!, 10 Oct 1999).

Material Examined: 3 spec., 12.4 × 4.7, 10.2 × 3.8, and 9.9 × 4.0 mm (Figure 36), at 4–10 m, Cabo de La Vela, Guajira Province, Colombia, A. Jorio and L. Couto! (author's coll.).

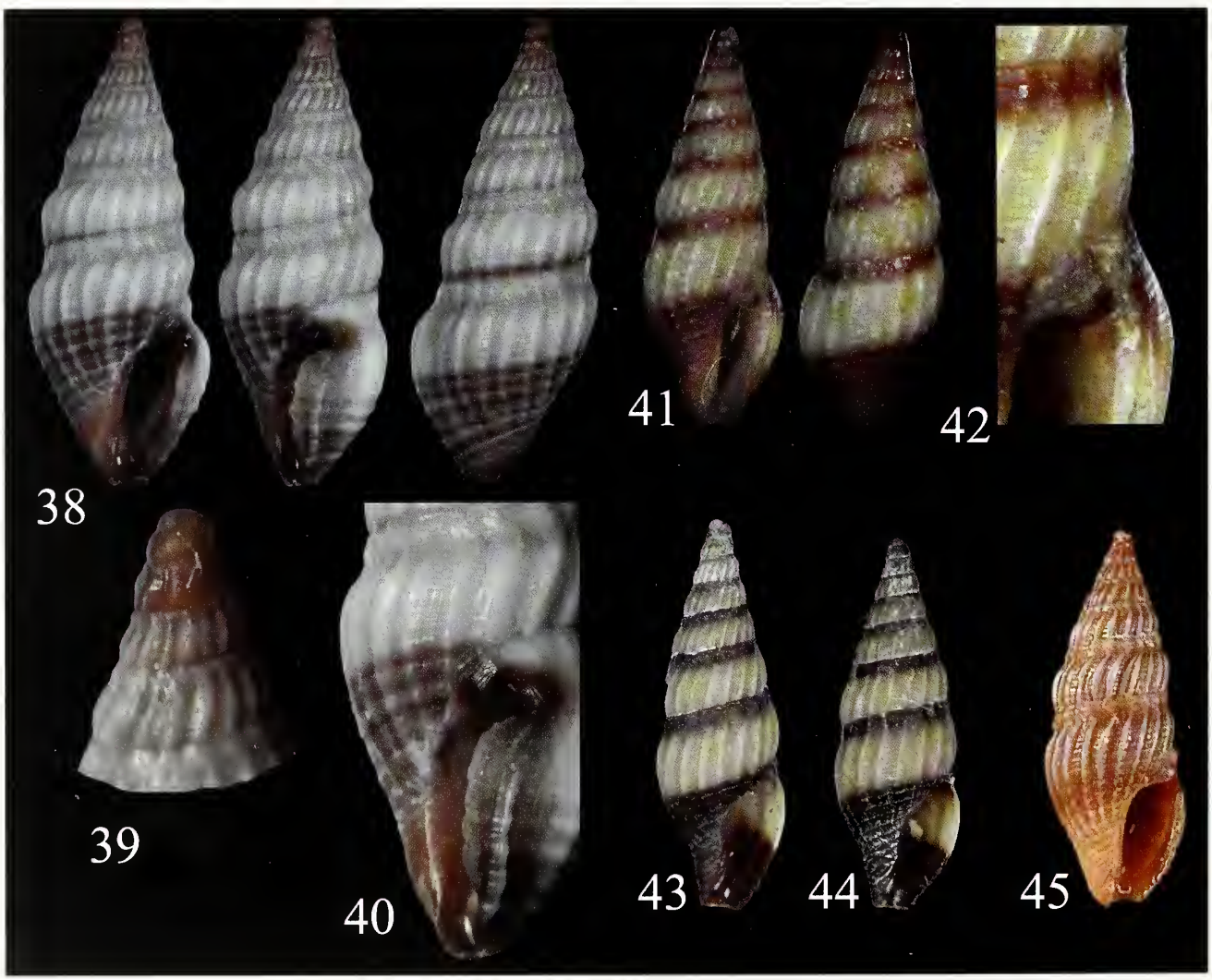
Range: Los Testigos Is., Venezuela, Cabo de la Vela, Guajira (locations "9" and "1", respectively, in Figure 1).

Remarks: A 9.6 mm specimen depicted on Femorale's Photo Gallery website (Coltro and Coltro, 1999) from Los Monges, Venezuela, may be this species (Figure 37, location "2" in Figure 1). A very similar but undescribed species from La Tortuga I., Venezuela (location 7 in Figure 1) is shown in Figure 45. *Crassispira mackintoshi* is closest to *C. multicostata* but differs in the arrangement of spiral threads in the sulcus, and has fewer axial ribs. It differs from *C. affinis*, *C. asthenes*, *C. masinoi*, and *C. blanquilla* in having a shallower, narrower anal sulcus and a more compact-oval shape. It is also a different color, dark gray with white axials, not yellow as in *C. affinis*, or uniformly light brown as in *C. asthenes*, or honey-colored as in *C. masinoi*, or creamy white as in *C. blanquilla*.

Etymology: Named for one of the collectors of the type specimens, and most of the specimens presented in this paper, Gary Mackintosh.

Crassispira (*Crassiclava*) *cana* new species
(Figures 38–40)

Description: Holotype 11.4 × 4.4 mm, fusiform, of 8.5 strongly convex whorls; axial sculpture predominant. Suture appressed, slightly scalloped by underlying ribs of preceding whorl; sulcus excavated, about 0.25 height of spire whorl (Figure 38). Body length 57% of total shell length. Protoconch paucispiral, of 2 smooth but not glossy whorls, last 0.5 whorl with 8–9 fine riblets



Figures 38–45. *Crassispira* spp. **38–40.** *Crassispira* (*Crassiclava*) *cana* new species. **38.** Holotype, USNM 1154269, 11.4 × 4.4 mm. **39.** Holotype, enlarged view of protoconch. **40.** Holotype, enlarged view of anterior lateral half. **41–44.** *Crassispira* (*Crassiclava*) *vexillum* (Reeve, 1845). **41.** Holotype, NHMUK 1900.3.9.38, 9.7 × 3.5 mm. **42.** Holotype, enlarged view of parietal callus. **43.** USNM 1154270, Young I., SVG, 9.6 × 3.2 mm. **44.** FLMNH 446788, Young I., SVG, 9.1 × 3.1 mm. **45.** *Crassispira* (*Crassiclava*) sp. Unidentified species from off La Tortuga I., Venezuela, 9.3 mm (photograph courtesy Femorale).

(Figure 39). Axial sculpture of fine, slightly opisthocline axial ribs, hooked to the left in sulcus, with ends swollen near suture; some ribs finely, unequally bifurcated on shell base; 19 axial ribs on the penultimate whorl, 16 on last whorl to varix. Microscopic growth striae in sulcus, also hooked to the left. Spiral sculpture of indistinct and irregularly spaced shallow incised lines between ribs, absent on rib crests, more closely packed in sulcus. No subsutural cord. Shell base with 5–6 evenly spaced flattened spiral cords, nodulose at their intersection with axial ribs. Five spiral cords on anterior fasciole. Outer lip thin, projects out from a thickened varix, slightly scalloped by the spiral cords; reinforced by a rib; shallow stromboid notch present (Figure 40). Varix broad and swollen, positioned a little behind the anal sinus. Anal sinus deep, U-shaped, bordered by the parietal callus. Inner lip is narrow, appressed to columella; thickened anteriorly, and posteriorly into heavy parietal callus where it joins the outer lip. Shell color white with dark purple-brown shell base, which is incompletely overlapped by succeeding whorls; aperture dark purple-brown. Rib crests, some spiral cords, and varix white; shell apex, anterior canal, and fasciole brown, not purple-brown.

Type: Holotype: USNM 1154269.

Type Locality: Aves de Sotavento, Las Aves archipelago, Federal Dependency, Venezuela, in 7–10 m.

Range: Known only from the type locality (location "6" in Figure 1). Both specimens shown on the Femorale's Photo Gallery website (Coltro and Coltro, 1999: numbers 37594 and 42682) are from Sotavento, Las Aves, and were collected by G. Mackintosh Oct 1998 (M. Coltro pers. comm. 29 Sep 2009).

Remarks: *Crassispira cana* is unique in its coloration among *Crassiclava*. From *C. affinis* it also differs in lacking subsutural spiral threads and in having only a few spiral incised lines overriding the ribs. *Crassispira affinis*, has less distinct ribs, and less distinct axial rib traces in the sulcus. From *C. blanquilla* it differs in having fewer axials (19 vs. 22–25 on their respective penultimate whorls); from *C. mackintoshi* it differs in being broader, in having a wider sulcus, fewer axials (19 vs. 24–31 on the penultimate), and lacking spiral elements in the sulcus. From *C. vexillum* it differs in having more convex whorls giving it a more shouldered appearance, a broader sulcus with heavier rib traces, stronger spiral cords on the shell base, and the crests of ribs and cords on the body are white—not the same color as the band, as is the case with *C. vexillum*.

Etymology: White-capped *Crassiclava*. "*Cana*" is the feminine form of the Latin adjective *canus*, one of whose meanings is white-capped (Oxford Latin Dictionary). The peculiar coloring of this species, which appears to be a consistent trait, brings to mind a snow-capped peak.

Crassispira (*Crassiclava*) *vexillum* (Reeve, 1845)
(Figures 41–44)

Pleurotoma vexillum Reeve, 1845: pl. 29, fig. 264: Higgins and Marrat (1877); Paetel (1888).
Drillia vexillum (Reeve, 1845): Tryon (1884: 209, pl. 13, fig. 72).
Crassispira vexillum (Reeve, 1845): Maes (unpublished, per Rosenberg, 2009); Williams (2005: number 3117).
Not *Drillia vexillum* (Reeve, 1845): Hidalgo (1904) and Hedley (1913) for Indo-Pacific species.

Description: Holotype 9.7 × 3.5 mm, narrowly fusiform, of 8 slightly convex whorls; suture appressed; sulcus narrow, flat to slightly convex, approximately 0.25 height of whorl; body whorl 65% of the total length; axial sculpture predominant (Figure 41). Other examined specimens are 9.1–9.6 mm in length, with immature lips. Protoconch of holotype worn, the 9.6 mm specimen (USNM 1154270) has 2 smooth dark brown whorls and few weak axials on last 0.25 whorl. Axial sculpture consists of narrow, well defined and slightly opisthocline ribs, reduced in sulcus to fine arcuate lines, ends swollen near the suture. Ribs evanesce on shell base; number 19 on penultimate and 13 to varix on body whorl of holotype, 18 on penultimate on other 2 examined specimens. Spiral sculpture in sulcus of threads, heaviest near suture, and together with swollen axial ends form nodulose subsutural fold. Spiral threads present on remainder of whorl, but fade on rib crests; approximately 5 well-spaced spiral cords on body whorl slightly nodulose at intersection with axials, with very fine threads between them. Six or 7 spiral cords on anterior fasciole. Outer lip broken, partially missing in holotype; with U-shaped anal sinus and large parietal lobe; stromboid notch not evident on broken lip. Aperture narrowly oval; anterior canal short, open. Shell color ivory white with chocolate-colored band anteriorly, and narrower one on sulcus; color shows through inside shell aperture.

Type: Holotype: NHMUK 1900.3.9.38.

Type Locality: Unknown to Reeve; herein designated as Young I., St. Vincent and the Grenadines.

Material Examined: 1 spec. 9.6 × 3.2 mm (Figure 43), at 4.6–10.7 m, Young I., SVG, G. Mackintosh!, 1998 (USNM 1154270); 1 spec., 9.1 × 3.1 mm (Figure 44), at 4.6 m, Young I., SVG, G. Mackintosh!, 3 Sep 2000 (FLMNH 446788). Only photographs of the following were examined: Femorale's Photo Gallery website species 62659 (Coltro and Coltro, 1999), 10 mm, at 50–70 m, Bequia I., SVG (Carlos Henckes, pers. comm., 20 Jul 2009); Williams (2009: number 3117), Young I., SVG (Peggy Williams, pers. comm., 20 Jul 2009).

Range: St. Vincent and the Grenadines (Young I., and Bequia I.), location "12" in Figure 1. No specimens have been found in museum collections or in more recent publications to confirm Barbuda as a valid locality as reported by Higgins and Marrat (1877).

Remarks: *Crassispira vexillum* is easily distinguished from other *Crassiclava* by its small size (usually less than 10 mm in length), narrowly fusiform shape, and unique

coloration. The chocolate-colored banding is present on all specimens examined, and on all others seen in photographs. Its inclusion in *Crassiclava* is based on the presence of a heavy parietal lobe at the front of the anal sinus, thin axial ribs that extend from suture to suture, spiral threads confined to rib interstices except on the shell base, and a weakly formed subsutural cord.

Reeve described this species without locality. Higgins and Marrat (1877) included this taxon among the specimens taken in the Argo Expedition to the West Indies in 1876. The first modern worker to recognize this as a Western Atlantic species, over 130 years after its original description, was V.O. Maes (unpublished, per Rosenberg, 2009). Since then, specimens have been figured by Williams and on the internet on Femorale's Photo Gallery (Coltro and Coltro, 1999), and all reportedly found around St. Vincent I., the type locality assigned herein. In addition to St. Vincent, Higgens and Marrat (1877) listed Barbuda as a locality, but this cannot be verified as the whereabouts of their specimens have not been found.

Tryon (1884: 209) lists this species from Port Jackson, Australia. Hidalgo (1904) and Hedley (1913), also list the species from the Indo-West Pacific. No subsequent references citing occurrence of this species in the Indo-Pacific have been found in the literature, so these reports are interpreted as misidentifications or miss-localizations, especially in light of the close match to Reeve's type of specimens collected from SVG in recent years.

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DNA barcoding reveals *Brachidontes* (Bivalvia: Mytilidae) from two ecologically distinct intertidal habitats on Long Key, Florida Keys, are cryptic species, not ecotypes

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ABSTRACT

The nominal morphospecies *Brachidontes exustus* (Linnaeus, 1758) represents a cryptic species complex with multiple genetic disjunctions resulting in regionally dominant, but range-restricted, species throughout the western Atlantic, Caribbean, and Gulf of Mexico. In the Florida Keys, four species were previously identified using molecular techniques. Specimens were collected in January 2005 from two distinct habitats, a seawall and a mangrove, on Long Key, Florida Keys. The locations are separated by <5 km. Eight specimens from the mangrove and four from the seawall were sequenced for the mitochondrial COI gene. Two seawall specimens were sequenced at the internal transcribed spacer 2 (ITS-2), in the nuclear ribosomal gene cluster, after the COI sequences appeared to be from the male mitochondrial line. The COI and ITS-2 sequences indicate that the two locations on Long Key, Florida Keys, have different single-species populations. The four seawall specimens were the Antillean species while the eight mangrove specimens were the Gulf species. Given that these mussels broadcast spawn, with subsequent planktotrophic larval development, the sites likely share a common pool of potential larval recruits. Single-species populations at each location are suggestive of habitat partitioning, ecological filters, or differential recruitment.

Additional keywords: Brachidontes, cryptic species, Florida Keys, cytochrome *c* oxidase subunit I (COI), DNA barcoding

INTRODUCTION

The seorehed mussel, *Brachidontes exustus* (Linnaeus, 1758), is a small bivalve (maximum length = 25 mm) in the family Mytilidae that eommonly inhabits rock pilings, seawalls, and wharf pilings in the intertidal zone and is most abundant in the lower intertidal (Seed, 1980). Abbott (1974) considered *B. exustus* and *Braehidontes domingensis* (Lamarck, 1819) separate species with the range of *B. exustus* from North Carolina to Texas and the West Indies and *B. domingensis* from Bermuda, the Bahamas, and southeast Florida and throughout the Caribbean. Later authors (Rios, 1985; Jensen and Harasewych, 1986) introdueed taxonomic confusion by reciproeally synonymizing the two names. Rios (1985), working in Brazil, eonsidered *B. exustus* the primary name and *B. domingensis* a synonym. Jensen and Harasewyeh (1986), publishing in a volume on the fauna of Bermuda, used the more reeent *B. domingensis* as the primary name. Although these authors were working at opposite ends of the range and designated a different primary name, the combined eonelusions suggested that a single intertidal *Braehidontes* species spans the entire range from North Carolina to Argentina.

This morphospeeies has been shown to be a eryptic species complex throughout its western Atlantic, Gulf of Mexieo, and Caribbean Basin range. Five moleeular taxonomic units (MTU) within the nominal species have been identified using nuclear and mitochondrial gene trees. Each MTU has been given an informal name corresponding to its eore geographical distribution; Antilles, Atlantie, Bahamas, Gulf, and Western Caribbean (Lee and Ó Foighil, 2005). Four of these eryptic speeies (Antilles, Atlantie, Bahamas, and Gulf) have been found in the Florida Keys (Lee and Ó Foighil, 2004). The four speeies are nested, two sister-speeies apiece, within two of the three main branches revealed by a ribosomal 28S gene tree (Lee and Ó Foighil, 2005). The five eryptie speeies have not yet beeu formally described and currently remain under the single morphospeeies taxon, *Braehidontes exustus*.

DNA barcodes have been proposed as a method for genetieally cataloging the world's biologieal diversity

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(Hebert et al., 2003). The proposed "barcode" is a short section of the mitochondrial genome that can identify unknown specimens when compared to an existing database of sequences, and are particularly useful in identifying cryptic species (Hebert et al., 2004; Gomez et al., 2007) or other closely-related species (Packer et al., 2009). The 5′ region of the cytochrome *c* oxidase subunit I (COI) mitochondrial gene, amplified by the well-known "universal" COI primer pair of Folmer et al. (1994), has emerged as the agreed-upon sequence for DNA barcoding for most species. Some bivalves have a unique mitochondrial inheritance system that may complicate the effectiveness of DNA barcoding. Doubly uniparental inheritance (DUI) of sex-linked mitochondrial lineages (Zouros et al., 1994; Mizi et al., 2005) results in maternally and paternally-inherited mitochondrial genomes coexisting in males. DNA barcodes that do not match the known sequences of the species may result if tissues used for DNA extraction are enriched with the male line of mitochondria.

Lee and Ó Foighil (2004) collected nominal *Brachidontes exustus* from three rocky intertidal sites from the Florida Keys (Figure 1). The Bahamian and Gulf species were most commonly encountered. The Bahamian species dominated their most southerly collection site at Boca Chica Key, while the Gulf species was most common at the Horseshoe site on Spanish Harbor/West Summerland Key, though intermingled with individuals of the Bahamian species. The Atlantic and Antillean species were much less common and were identified from very few individuals. The only genetically verified records of these two presumably rarer species include a single Atlantic species specimen found with an otherwise Bahamian population at Boca Chica Key, and three sub-adults of the Antillean species found along with five Bahamian species individuals at Key Biscayne (Lee and Ó Foighil, 2004). Lee and Ó Foighil (2004) did not collect specimens from mangroves, a habitat for *B. exustus* encountered by Bennett and Willan (2003) in the Florida Keys, and subsequently by Lee and Ó Foighil (2005), where they found the Western Caribbean and Atlantic species in a mixed population.

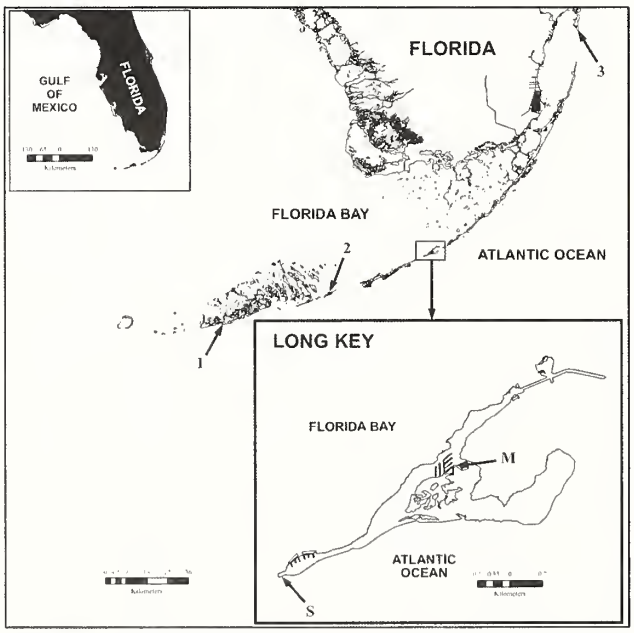


Figure 1. Map of the Florida Keys showing the collection locations of Lee and Ó Foighil (2004). 1 = Boca Chica Key, 2 = The horseshoe site on Spanish Harbor/West Summerland Key, and 3 = Key Biscayne. Upper left inset showing the Floridian peninsula. Lower left inset showing Long Key and collection locations of this study. S = seawall habitat location and M = mangrove habitat location.

Sibling species and cryptic species complexes in what were previously believed to be single species are well known for many marine taxa (Knowlton, 1993), including bivalves (Marko and Moran, 2009). In the *Mytilus* complex of *M. californianus*, *M. galloprovincialis*, and *M. trossulus* on the western coast of North America, the distributions appear to be maintained by subtle habitat differences that influence local post-recruitment dominance (Heath et al., 1995; Johnson and Geller, 2006). Likewise, local habitat differences may influence *Brachidontes* cryptic species distributions in the Florida Keys. The goal of the present study was to determine the species distribution in the two distinct habitat types on Long Key, where *B. exustus* was encountered. A previous study of Floridian *Brachidontes* spp. (Lee and Ó Foighil, 2004) did not include specimens from seawall or mangrove habitats, nor were multiple samples taken from different habitat locations on a single island.

MATERIALS AND METHODS

Study Area

Long Key, a 6-km long Y-shaped island in approximately the middle of the Florida Keys archipelago, has an interior lagoon fringed by mangroves with a connection to the bayside of the island (Figure 1). The nearest mile marker on US Route 1 serves as a useful universal landmark for the Florida Keys and the number of the nearest mile marker is included with the collection locations. Mile marker 0 corresponds to the western edge of Key West, and the mile number increases as one moves east and north towards mainland Florida.

The first collection location (latitude 24°48.10 N, longitude 80°50.58 W) is an ocean-side vertical concrete seawall near mile marker 66 at the west end of Long Key, adjacent to the Long Key Viaduct (Figure 1). The lowest intertidal zone of the seawall is approximately 1 m above a sandy bottom. Wave exposure at this location is high and directly impacts the exposed substrate. The second collection location (latitude 24°49.22 N, longitude 80°48.45 W), near mile marker 68 and approximately 4 km to the northeast, is a mangrove-lined boating channel that leads from the bayside of the island to the interior lagoon and is protected from direct wave action.

Sample Collection

Living specimens were collected in January 2005. Four small individuals approximately 11 mm in length were found in the lower intertidal on the seawall and all were collected. A total of 46 individuals ranging in size from 6 mm to 22 mm were collected from an abundant population in the mangrove habitat. All specimens were immediately transferred to a seawater flow-through system and maintained alive for several days before being frozen at −40°C. The samples were subsequently transported on dry ice and stored at −80°C prior to dissection and molecular characterization.

Specimens were thawed to room temperature, dissected, and the soft tissues separated from the shell. The disarticulated left valve of each subsequently typed specimen was photographed using a Nikon digital SLR camera mounted on a Zeiss Stemi 2000-C dissecting scope.

DNA Extraction and Molecular Characterization

Total genomic DNA was isolated from approximately 20 mg of tissue from either the posterior adductor muscle in larger specimens or mantle tissue in smaller specimens. The extraction was accomplished with a DNeasy Tissue Kit (Qiagen, Valencia, California) according to the manufacturer's instructions. Extracts were stored at −20°C until used as PCR templates.

The target fragment for DNA barcodes, the 5′ end of the cytochrome *c* oxidase subunit I (COI) gene from the mitochondrial genome, was amplified by polymerase chain reactions (PCR) using Taq PCR Mastermix (Qiagen, Valencia, California) and the well known "universal" COI primer pair, LOC 1490 and HOC 2198, from Folmer et al. (1994) with a thermal cycler protocol of 3 min initial denaturing at 95°C followed by 35 cycles of 95°C for 1 min, 40°C for 1 min, 72°C for 1.5 min, with a final 7 min extension at 72°C.

A second target fragment, the second internal transcribed spacer (ITS2) region from the nuclear ribosomal gene cluster, was sequenced for two specimens from the seawall for reasons discussed below. The ITS-2 was amplified with the forward primer (5′-CATCGATATCTTGAACGC-3′) from Lopez-Piñión et al. (2002) initially designed for European scallops and the reverse primer (5′-GCTCTTCCCGCTTCACTCG-3′) from Xu et al. (2001) initially designed for various species of *Crassostrea*. The thermal cycler protocol was 3 min initial denaturing at 94°C followed by 30 cycles of 94°C for 30 s, 55°C for 30 s, and 72°C for 60 s with a final extension of 5 min at 72°C. All reactions were prepared in 50-µl volumes and a negative control containing all reagents and the primer pair, without the DNA template, was included with each amplification series. The resulting PCR products, controls, and a 100-bp ladder were run on a 2% agarose gel, stained with ethidium bromide, and photographed under UV transillumination.

PCR products were checked for the appropriate size, purified with a MinElute kit (Qiagen, Valencia, California) according to the manufacturer's directions and subsequently directly cycle-sequenced in both directions with the above amplification primers utilizing the BigDye Terminator v.3.1 Cycle Sequencing kit (Applied Biosystems, Forester City, California) and an automated DNA sequencer (310 Avant Genetic Analyzer, Applied Biosystems, Forester City, California).

Chromatograms of sequences were edited manually by comparing both strands in 4Peaks (by Griekspoor and Groothuis, Mekentosj.com). The edited sequences were compared to an existing database of sequences using the Basic Local Alignment Search Tool (BLAST) (Altschul et al., 1990) of the National Center for Biotechnology Information (NCBI). The most significant alignment with the highest percent congruence to published sequences was treated as the species identification.

Gene Tree

A subsample of COI sequences representing each of the five cryptic species and their within-species diversity from their total geographic range were obtained from GenBank (accession numbers AY621879, AY621909, AY621911, AY621913, AY621914, AY825105, AY825201, AY825202, AY825204 and AY825216) (Lee and Ó Foighil, 2004; Lee and Ó Foighil, 2005) and combined with nine of the ten newly generated maternal COI sequences. The sequences were aligned in Clustal X and a gene tree was created using the neighbor-joining method.

RESULTS

Species Assignment from Sequences

The gene tree created from the seven mangrove and two seawall specimen COI sequences and select COI sequences obtained from GenBank show the relationships of the specimens to the five cryptic species within the complex (Figure 2). Two specimens from the seawall location were excluded as explained below. Table 1 shows species identifications based on comparisons to the NCBI database for all sequences generated in this study.

Seawall Location

The resulting COI sequences, when compared to the NCBI database, had closest matches to an Antillean species sequence and a Biscayne clade species sequence. The Biscayne clade was later named the Antilles species after gene trees from the full western Atlantic and Caribbean range showed that some specimens initially collected from Key Biscayne during the sampling of Lee and Ó Foighil (2004) were related to the dominant species of the Antillean archipelago (Lee and Ó Foighil, 2005). The match to an Antillean COI sequence was 100% for two of the four specimens (Lee and Ó Foighil, 2004; Lee and Ó Foighil, 2005). The two other sequences were hard to clean and edit because of many instances of unclear peaks in both the

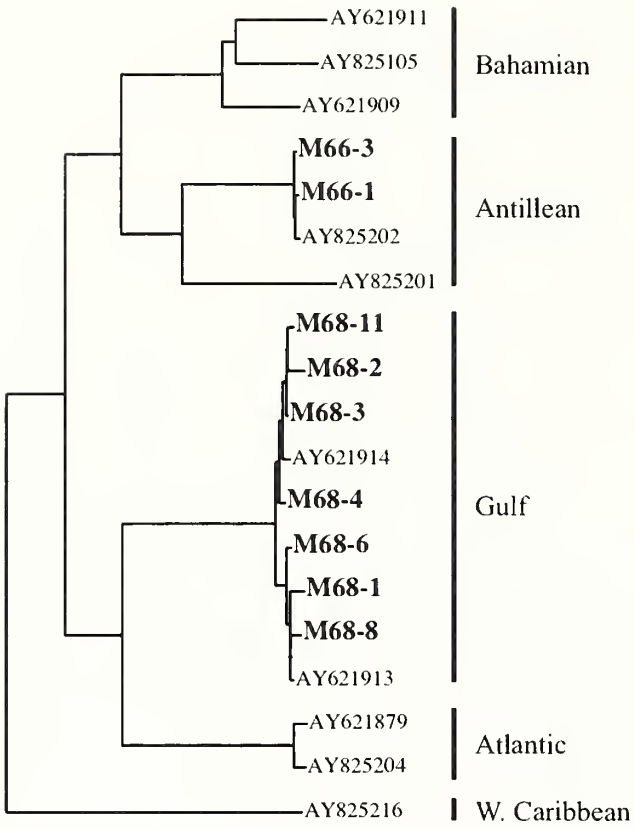


Figure 2. Phylogram generated from DNA sequences of the COI gene from representatives of cryptic species within the *Brachidontes exustus* morphospeices complex. GenBank sequence numbers and corresponding cryptic species are labeled. The mile location and specimen number labeling the sequences generated in this study are in bold.

forward and reverse sequences. The two cleaned and edited sequences had sections at both ends that were ambiguous, which were cropped from the full sequence before being compared to the NCBI database. The two sequences were 543 and 621 nucleotides long and returned respectively an 82% and 83% closest match to GenBank accession number AY621945, a male mitochondrial line COI sequence of a Bahamian species specimen collected at Boca Chica Key (Lee and Ó Foighil, 2004). The most congruent non-male COI sequence match for both specimens was an Antillean species sequence–AY825208 (Lee and Ó Foighil, 2005), with 80% congruence.

The specimens that yielded the presumptive male COI sequence were subsequently sequenced at the ITS-2 locus to determine their species identity. The resulting sequences were 355 nucleotides long and when compared to the NCBI database returned either 100% or 99% congruence with AY621970. Sequence AY621970 is the complete sequence of the internal transcribed spacer 2, and flanking portions of the 5.8S and 28S ribosomal RNA genes, obtained from voucher specimen 300123.6 of the University of Michigan Museum of Zoology. The specimen was collected from Key Biscayne, Florida (Lee and Ó Foighil, 2004). Both of the newly-generated ITS2 sequences contained a 4-nucleotide deletion relative to the Bahamian sequences at aligned location 130, a polymorphism consistent with the single Antillean species ITS2 sequence in GenBank, and lacking in any Bahamian species ITS2 sequence. The four seawall specimens are thus grouped with the Antillean species, by either mitochondrial COI or nuclear ITS-2 sequences. The Antillean species is one of the two less common species encountered by Lee and Ó Foighil (2004) in the Florida Keys and this new record more than doubles the confirmed number of individuals of this species collected in South Florida.

Mangrove Location

Eight specimens from the mangrove location were chosen for sequencing based on extremes in size and shape revealed by a Principal Components Analysis based on shell morphometrics (unpublished data). The expectation is that if more than one species is present at this location the extremes of size and shape would likely include representatives of the cryptic species. COI

Table 1. Specimen, habitat type, sequenced gene, fragment length in nucleotides used for database comparisons, NCBI accession number of sequence with most significant alignment, percentage congruence of *de novo* sequence to NCBI sequence, and resulting species identification of specimen based on closest matching sequence.

Specimen	Habitat	Gene	Length	Significant alignment	Congruence	Species
M66-1	seawall	COI	660	AY825154	100%	Antilles
M66-2	seawall	ITS-2	355	AY621970	99%	Antilles
M66-3	seawall	COI	660	AY621849	99%	Antilles
M66-4	seawall	ITS-2	355	AY621970	99%	Antilles
M68-1	mangrove	COI	660	AY621885	99%	Gulf
M68-2	mangrove	COI	660	AY621915	99%	Gulf
M68-3	mangrove	COI	660	AY621915	100%	Gulf
M68-4	mangrove	COI	660	AY621897	99%	Gulf
M68-5	mangrove	COI	474	AY621915	99%	Gulf
M68-6	mangrove	COI	660	AY621913	99%	Gulf
M68-8	mangrove	COI	660	AY621913	99%	Gulf
M68-11	mangrove	COI	660	AY621915	99%	Gulf

sequences of seven specimens were 660 nucleotides long and when compared to the NCBI database returned in all cases a Gulf species closest match with 100% or 99% congruence (Table 1). The COI sequence of one individual, M68-5, had many ambiguous peaks at both the 5′ and 3′ ends and a clean sequence of 474 nucleotides was excised from the longer sequence. This 474-nucleotide-long fragment was compared to the NCBI database and returned 99% congruence to a Gulf species COI sequence. The shorter COI sequence was not included in the gene tree, but nonetheless serves as a positive identification of this specimen as the Gulf species.

DISCUSSION

One major criticism of DNA barcodes as a method of species designation is the possibility of misidentifications based on errors in the database of linked sequences. This is a problem with using GenBank data, where a submitter of the sequence names the taxon to which the sequence is linked. There is no outside review of the validity of the taxonomy and only the original submitter can change the name attached to the sequence. *B. exustus* appears to suffer from just such a problem. The linked taxon in the NCBI database is *Hormomya exustus*, a generic name long ago synonymized to *Brachidontes exustus* (Soot-Ryen, 1969). This problem in taxonomy now extends to the Barcode of Life Database (BOLD) by virtue of its linking to the NCBI database. BOLD utilizes only a standardized 648-nucleotide fragment from voucher specimens whose origin and current status are recorded (Hebert and Gregory, 2005). Additionally, without the proper taxonomic treatment of the cryptic species, there is no way to know that cryptic species are involved without a detailed knowledge of the clade information included for each *Brachidontes* specimen in the GenBank database. While the BOLD attempts to be more rigorous than the GenBank database because voucher specimens are required for each sequence, the lack of taxonomic treatment for each of the cryptic species within the *Brachidontes exustus* complex likely dooms them to obscurity until a proper taxonomic treatment is undertaken (Schlick-Steiner et al., 2007).

Lee and Ó Foighil (2005), remarking on the distributions of the five *Brachidontes* species throughout the entire known Atlantic, Gulf of Mexico, Bahamas, and Caribbean range, note that the Gulf/Atlantic clade appears mostly on continental margins, while the Bahamas/Antilles clade is found predominately on oceanic islands. The abiotic aspects of the mangrove habitat may be more similar to continental margins, while the seawall habitat may be more similar to the conditions found on oceanic islands. Distinct differences between the bivalve species assemblages on the bay and ocean-sides of the Florida Keys archipelago are known (Bieler and Mikkelsen, 2004; Mikkelsen and Bieler, 2007) and the distribution of *Brachidontes* spp. on Long Key are likely representative of the same environmental factors that influence other bivalve species' distributions. Furthermore, the environmental conditions of the core distributions of the individual *Brachidontes* species in the western Atlantic, Gulf of Mexico, Bahamas, and Caribbean Sea observed by Lee and Ó Foighil (2005) relate to the conditions coinciding with the species' distribution on Long Key. High salinity and low productivity associated with ocean islands are present at the seawall, while lower salinity and high productivity conditions associated with continental margins are present at the mangrove site.

Only four individuals were found on the approximately 250 m of seawall after considerable effort and all individuals were collected and used for genetic typing. Based on the very low abundance and small size of the collected specimens, this location likely represents a marginal habitat for *Brachidontes* spp., survivable by only one of the species within the complex. The four seawall individuals were only half the maximum length of individuals found in the mangrove habitat yet they are likely sexually mature. Mytilids have doubly uniparental inheritance of sex-linked mitochondrial lineages (DUI) (Zouros et al., 1994) and the initial extraction appears to have been contaminated by sperm from a portion of gonadal tissue extracted with the mantle tissue. Only sexually mature males would have sperm in sufficient quantities to make a significant contribution of the paternally-inherited COI sequence to the PCR amplification. The smallest reproductive individuals encountered during a study of the gametogenic cycle of *B. exustus* (presumably the Atlantic species) at Wassaw Island, Georgia were about 10 mm long (Sweeney and Walker, 1998). This is slightly smaller than the specimens collected from the seawall on Long Key. If the threshold for reproductive size is similar for the Atlantic and Antillean species, then the seawall specimens are within the known limits of size for reproductive individuals.

The presumptive male sequences are slightly less congruent with the Antillean species maternal COI line (80%) than they are with the known male COI sequences (82%) from Bahamian specimens. An alignment of the two new presumptive male sequence fragments in Clustal X showed the sequences to be very close to each other with few single nucleotide substitutions and one section of over 100 nucleotides identical between the two sequences. The close congruence suggests that the sequences are not amalgamations of amplified maternal and paternal COI PCR products but are the sequences for the male COI of the Antillean species. In other bivalves that display DUI the male mitochondrial genome has been hypothesized to have been replaced and reset to the female mitochondrial line (Mizi et al., 2005). The similar 20% differences between the Bahamian male COI and the maternal Antillean species COI may be a result of a resetting of the male COI line to the maternal mitochondrial line after speciation. A fuller gene tree comprising the male COI sequences of each species within the complex would answer the

questions of male mitochondrial genome origins. Contamination by mitochondrial DNA from sperm would not affect the amplification of the nuclear ITS-2 used for the species designation of the two specimens that yielded a presumptive male COI sequence.

Ideally, a range of size classes from the seawall location would have been used for species identifications, but all four of the specimens found on the seawall were approximately 11 mm in length. Wave exposure at the seawall is a prominent environmental feature and could be limiting abundance and survival at the seawall. At Moss Landing, California, and along the central coast of California, *Mytilus* spp. occurs in mixed populations in which the dominant species differs among age classes. When wave exposure is more intense, one species of *Mytilus* comprises a greater proportion of adults than juveniles, suggesting that the adults of this one species are more resistant to dislodgement by wave action (Heath et al., 1996; Johnson and Geller, 2006). Wave exposure may play a role in the species composition at the seawall location, although wave exposure alone cannot explain the observed pattern in the mangrove habitat. Antillean species individuals should be present in the mangrove, a habitat with low wave exposure, if wave-induced dislodgement were the only environmental attribute influencing the distribution.

The harsh conditions under high wave exposure may limit the growth or set a maximum attainable size for the few individuals that persist at the seawall. Alternatively, larger individuals may still be susceptible to dislodgement once over a certain size threshold. While all of the seawall specimens were about the same length, they may be of varying ages and not representative of a single settlement cohort because growth may slow to near zero under the stress of intense wave exposure.

Unfortunately, the small sample size at the seawall location and limited number of collection locations from Long Key truncate the explanatory power of this study. The inclusion of the apparently marginal habitat at the seawall for a study of species distributions in the Florida Keys became a necessity because many locations that seemed suitable for *Brachidontes* spp. did not have populations and specimens were collected whenever they were encountered. Nonetheless, the stark contrast of species-specific populations of cryptic species at such proximal locations and differing habitats warranted including such a marginal habitat for comparison. The only other record of the Antillean species in the Florida Keys is from a habitat at Key Biscayne with very low abundances of *Brachidontes* spp. (Lee and Ó Foighil, 2004). The Antillean species may be more common in the Florida Keys than the records to date suggest because marginal habitats have not been actively searched in the few existing studies on this species complex.

At the mangrove location, specimens were found as dense clusters of individuals within the byssal threads of another bivalve, *Isognomon* sp., which were, in turn, attached to the mangrove roots. It was not uncommon to find 20 or more individuals within the threads of a single *Isognomon* sp. Specimens were collected from the same mangrove location during the summer of 2002 but were not used in this study. Shell morphology over the 2.5-year period remained consistent and the largest shells from the two collection times were about the same length ($\approx$ 25 mm). Unlike the individuals collected from the seawall, the mangrove specimens identified by COI sequences spanned the entire range of sizes collected and the specimens chosen for sequencing were at the extremes of size and shape variation. If individual settlement events were dominated by a single species, there should be a change in the species composition at the various size classes and between the two collections times. Based on the consistent species designation by sequence data over the entire range of size classes, combined with the consistent shell morphology, it appears that the exclusivity of the Gulf species at the mangrove location was maintained over the 2.5 years between collections. This would be unlikely if the observed distribution were the result of stochastic larval settlement.

In contrast to the Long Key locations, other sites in the Florida Keys have more than one cryptic species of *Brachidontes exustus* coexisting on the same substrate (Lee and Ó Foighil, 2004). Neither of the Long Key collection locations was the rocky shore habitat sampled by Lee and Ó Foighil (2004). Mixed-species populations may reflect an overlap of suitable habitat that only exists at some rocky shore locations. Species may be contemporaneous on the same rocky shore by habitat partitioning, by depth, for example. Abiotic factors or biotic interactions could limit one or both species distribution on micro-scales in such a way to facilitate coexistence. Further investigation of the species' distributions, at spatial scales of individuals to islands, is warranted to elucidate the mechanisms of cocxistence or exclusion among the species within the complex.

Differential larval transport from single-clade source populations could potentially impact adult distributions. If the larvae of each species are not transported to all potential locations, the differences noted in the species distributions could be an artifact of larval transport processes and not ecological filtering. This seems unlikely given that *Brachidontes exustus* from the North American Atlantic coast, as well as the closely related species *B. granulata*, *B. modiolus*, and *B. variabilis*, broadcast spawn with planktotrophic larvae that can stay in the water column for up to 40 days before settlement (Campos and Ramorino, 1980; Fields and Moore, 1983; Morton, 1988; Fuller and Lutz, 1989). The planktonic larval phase would provide ample opportunity for tidal fluxes and currents to overwhelm any local larval source cohesiveness.

Studies of connectivity using biophysical modeling and elemental tracking suggest that long-range dispersal may be much rarer than simple assumptions of pelagic larval duration and ocean currents would indicate (Cowen et al., 2006; Becker et al., 2007). The four kilometers between the Long Key collection locations are well within the ecologically relevant magnitudes of

dispersal of 10 to 100 km of the Cowen et al. (2006) model and the 20 to 30 km suggested by experimental approach of Becker et al. (2007). Within the dispersal distances advanced by these researchers, larvae from both Long Key populations would have a very high likelihood of being delivered to the nearby location. Additionally, their results imply that larvae of all *Brachidontes* spp. present in the Florida Keys would be delivered to all suitable Florida Keys locations, suggesting that species-specific populations must reflect recruitment or post-recruitment processes and not clade-limited settlement events.

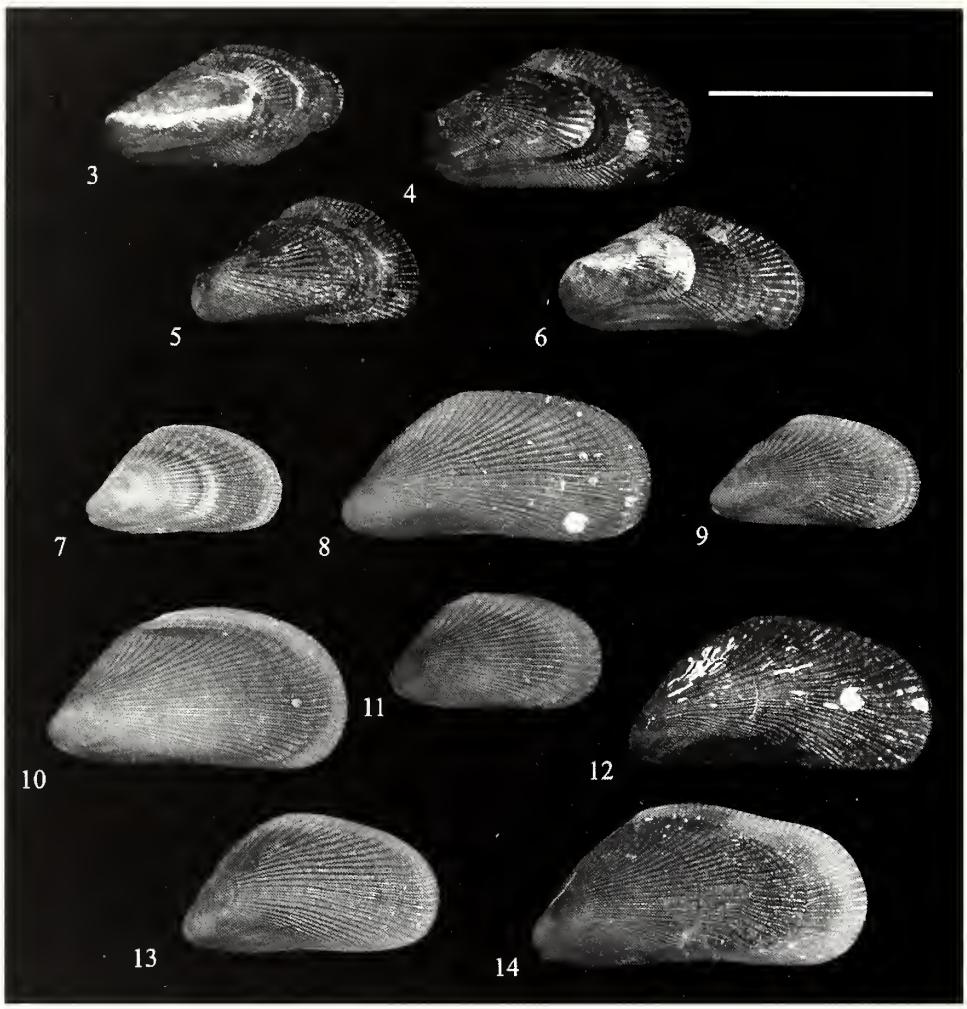
Previous authors (Lee and Ó Foighil, 2005) were unable to determine the species of a given individual by morphology alone. However, representative shell shapes are included in their nuclear and mitochondrial gene trees. A previous investigation of plasticity of *Brachidontes* spp. in the Florida Keys found large overlaps in the shell morphologies of specimens sampled from habitats with different wave exposures (Bennett and Wilan, 2003). Their conclusion of environmentally-induced plasticity is severely undermined by the discovery of the cryptic species complex in the Florida Keys. Two of Bennett and Wilan's collection locations, the Horseshoe site on Spanish Harbor/West Summerland Key and the mangrove on Long Key, do not have the same species distributions. The Horseshoe site has a mixture of Gulf and Bahamian species (Lee and Ó Foighil, 2004), while the mangrove location population is shown here to be limited to the Gulf species. The broad morphological variation that was observed at the sites sampled by Bennett and Wilan (2003) is probably the result of morphological differences between the cryptic species with the overlap in shell morphology between locations being the result of conserved Gulf species morphology. Regardless, the morphological variation observed does not reflect ecotypic differences within a single species.

Notwithstanding Lee and Ó Foighil's (2005) observations on morphology, there were some obvious qualitative differences in gross shell morphology between the specimens from the two Long Key locations. Shells collected from the seawall were thicker with more robust ribbing and were wider across both valves compared to shells of similar length collected from the mangrove habitat. When viewed laterally, the overall shell outline of the seawall specimens was more modioliform (Figures 3 through 6), while the mangrove specimens were more mytiliform (Figures 7 through 14). For the seawall specimens, the anterior margin was more rounded, the umbo in a more dorsal orientation, and the overall ventral-dorsal margin angle less than in specimens of similar size from the mangrove. These morphological differences match the known phenotypic plasticity of mytilids in habitats with different wave exposures (Seed, 1968), salinities (Nalesso et al., 1992), or shorelines (Morton, 1991). However, in light of the existence of cryptic species, it is unclear whether the observed morphological variation arises from phenotypic expression, genotypic constraints, or a combination of the two.

Multivariate statistical methods to determine species by shell morphometrics may be constructed with a large number of specimens that are unequivocally assigned to species by molecular methods. However, a statistical method is only possible if there are consistent genotype-dependent morphological differences that overwhelm any phenotypically-variable morphology. Sampling individuals from locations where the species coexist is the obvious starting point for examining this question because mussels from these locations should presumably be exposed to identical phenotype-inducing environmental cues and would be expected to display similar phenotypic responses. Any consistent morphological differences between the species at locations of coexistence would only be those whose expression is more dependent on genotype than phenotype. Morphological discrimination of cryptic species would make manipulation experiments possible because the mussels would not have to be killed in order to determine species. Reciprocal transplant or common-brood experiments could then be used to investigate the precise mechanisms regulating species survivability at single and multiple-species locations.

The discovery of cryptic species in such close proximity in the Florida Keys opens the possibility that hidden biodiversity within *Brachidontes* spp. populations may be found in other locations throughout the Caribbean if sampling efforts were increased. Most of the Caribbean island locations sampled by Lee and Ó Foighil (2005) were from a single collection site and yielded a single species. The two locations sampled on Trinidad, which yielded different species, provide an exception. While the two Trinidadian locations are about 20 km apart, the Atlantic species was collected at the town of Chaguaramas and the Antillean species was collected at Maracas Bay. Although the habitat types are not listed, habitat specificity similar to what was observed on Long Key may exist at these Trinidadian collection locations. Maracas Bay is on the north side of the island with an exposure to the Atlantic Ocean, while Chaguaramas is to the west, on the Gulf of Paria. The species distributions on Trinidad may be influenced by habitats with oceanic island and continental margin-like environments, as with the distributions observed at Long Key.

Many intriguing questions remain regarding the ecological mechanisms that affect the distribution of this cryptic species complex in the Florida Keys and the western Atlantic. More records of the species in close proximity may be discovered if sampling efforts are increased. Mangrove habitats in the Caribbean may support populations that are not the recognized dominant regional species. Understanding the mechanisms in specific habitats that maintain or exclude each species within the complex offers the potential to ask questions regarding interactions of very closely related species in the oceans. This little-studied complex may become a good model to investigate these types of difficult to answer questions.



Figures 3–14. Disarticulated left valves of 12 specimens from two sample locations on Long Key. Figure numbers of each shell are at the umbo. Shells in Figures 3 to 6 were collected from the seawall habitat, M66, and are the Antillean species. Shells in Figures 7 to 14 were collected from the mangrove habitat, M68, and are the Gulf species. Specimen codes for each figure are: 3) M66-1; 4) M66-2; 5) M66-3; 6) M66-4; 7) M68-1; 8) M68-2; 9) M68-3; 10) M68-4; 11) M68-5; 12) M68-6; 13) M68-8; 14) M68-11. Scale bar = 10 mm.

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A new *Sveltia* (Gastropoda: Cancellariidae) from off Guadeloupe, French West Indies

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ABSTRACT

Sveltia yoyottei, the first Recent species of *Sveltia* from the tropical western Atlantic, is described from bathyal depths off Guadeloupe, French West Indies. It is distinguished from its closest relative, *Sveltia inquilinus* (Jung and Petit, 1990) from the Pliocene of the Dominican Republic, by its shorter, more gradate spire, its narrower pseudoumbilicus, and by having fewer, stronger denticles along the outer lip. It differs from the Panamic *S. centrota* (Dall,1896) in having a smaller, narrower shell with 1–3 axial ribs between adjacent varices.

Additional key words: Pliocene, biogeography, paciphile.

INTRODUCTION

The cancellariid genus *Sveltia* is readily diagnosed on the basis of its biconical shell, moderately high spire, widely spaced axial ribs with an open spine at the shoulder, broad aperture, flaired peristome, and narrow pseudoumbilicus. *Sveltia* has a widespread geographic distribution in the Recent fauna, extending from western Africa to Argentina, the tropical and temperate eastern Pacific from Mexico to Chile, and New Caledonia. During the Pliocene, the range of *Sveltia* included most of western Europe. Following the discovery of *Sveltia inquilinus* (Jung and Petit, 1990: 91) from the Pliocene of the Dominican Republic, these authors added *Sveltia* to Woodring's (1966: 428) list of paciphile genera (genera once present in both the Caribbean and the western Pacific faunas that now survive only in the Pacific).

The discovery of a Recent species of *Sveltia* from Guadeloupe, described herein, reveals that the genus survives in the Caribbean Sea, and is not a paciphile genus.

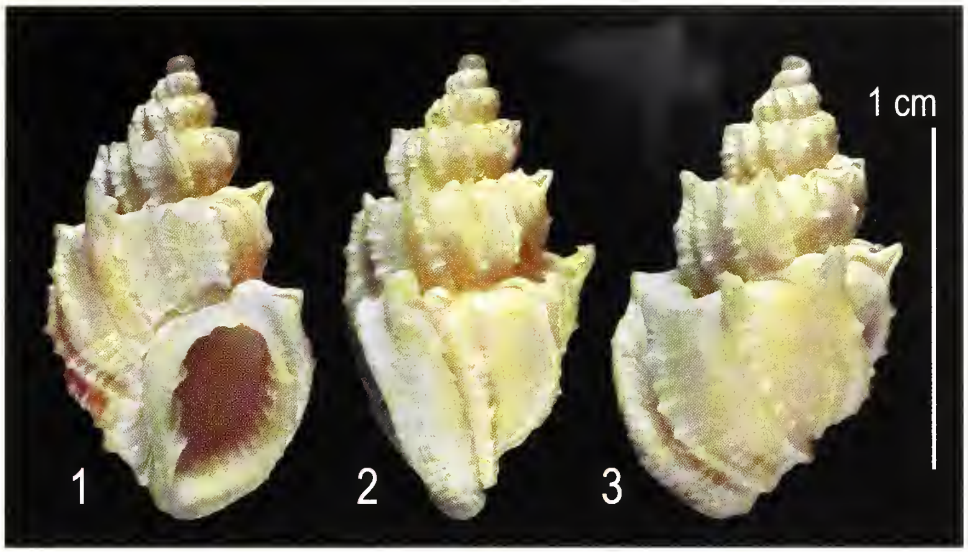
SYSTEMATICS

Family Cancellariidae Forbes and Hanley, 1851
Subfamily Cancellariinae
Genus *Sveltia* Jousseume, 1887: 214.

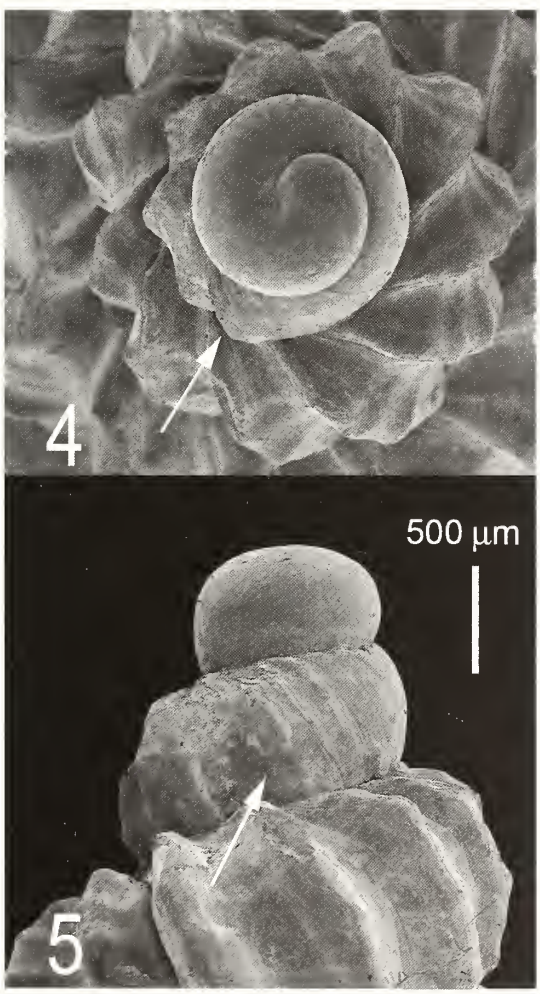
Type Species: "*Sveltia varicosa* Broec." (= *Voluta varicosa* Brocchi, 1814), by original designation.

Sveltia yoyottei new species
(Figures 1–3)

Description: Shell (Figures 1–3) small (to 13.6 mm), thick, with tall conical spire (spire angle 55°), rounded anterior, broadly ovate aperture with very short siphonal canal, narrow siphonal fasciole and pseudoumbilicus. Protoconch (Figures 4–5) paucispiral, increasing in diameter from 370 µm to 1.2 mm in 1½ inflated, smooth, glassy whorls, deviated from teleoconch axis by ~30°. Transition to teleoconch abrupt (Figures 4–5, arrows), marked by flared protoconch lip, onset of thick, shouldered prosocline axial ribs with weak spiral cords evident on ribs and shoulder. Teleoconch of 4 inflated, strongly shouldered whorls. Suture impressed. Axial sculpture dominant, of strongly prosocline ribs (9 on first postnuclear whorl, 11 on last whorl), with thicker, broader varices forming on every second then third rib starting with third teleoconch whorl. Two thick varices in close apposition appear to mark the end of growth (as in species of *Trigonostoma*, see Petit and Harasewych, 1987). Region between suture and shoulder with 0–1 fine threads, broadly flared on axial ribs and varices. Spiral sculpture of: strong open spines on ribs and varices along shoulder, 4–5 low, weak, narrow, rounded cords between shoulder and siphonal canal; 4 finer cords on siphonal canal, all producing knobs or weakly open spines on axial ribs and varices. Finer threads present between adjacent cords near the shoulder. Aperture broadly ovate, tapering anteriorly, deflected from coiling axis by 23°, surrounded by continuous, flared peristome, broadest along anterior third of outer lip. Outer lip with 10 short, rounded denticles. Inner lip with 2 denticles along parietal region. Columella thick, concave, with 2 strong columellar folds and a siphonal fold. Siphonal canal broad, indistinctly demarcated along outer lip. Shell cream colored, inside and out. Periostracum unknown. Operculum absent.



Figures 1–3. *Sveltia yoyottei* new species. **1.** Apertural, **2.** Lateral, and **3.** Dorsal views of the holotype, MNHN. Off Grande Terre, Guadeloupe, France, French West Indies, in 300 m.



Figures 4–5. *Sveltia yoyottei* new species. **4.** Apical and **5.** Lateral views of the protoconch of the holotype.

Type Locality: Off Pointe de la Grande Vigie, north Grande Terre, Guadeloupe, French West Indies, in 300 m.

Type Material: Holotype, Muséum national d'Histoire naturelle, Paris, MNHN 23684.

Etymology: This new species honors Mr. Jean-Claude Yoyotte, who collected the type specimen.

Comparative Remarks: *Sveltia yoyottei* it most similar to *Sveltia inquilinus* (Jung and Petit, 1990) from the Pliocene of the Dominican Republic from which it can be distinguished by its slightly shorter, more gradate spire, narrower pseudoumbilicus, and fewer, stronger denticles along the outer lip. *Sveltia inquilinus* has more inflated whorls with finer and more numerous spiral sculpture. The closest living relative of *S. yoyottei* appears to be *S. centrota* (Dall, 1896), which ranges from Baja California to the Galapagos. *Sveltia centrota* differs in having a much larger, broader, heavier shell with 8–10 evenly spaced varices per whorl, and lacks axial ribs between adjacent varices. *Sveltia yoyottei* also resembles *Sveltia zalmi* (Böse, 1910) from the Pliocene of Tehuantepee, Mexico, a precursor of *S. centrota*. However, *S. zalmi* has a taller, narrower shell with a more sharply angled shoulder with fewer varices, and a smaller, narrower aperture.

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Not a "living fossil:" the eastern Pacific bivalve *Tellidorella* belongs with Lucinidae, not Cardiniidae

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ABSTRACT

Tellidorella (type species: *T. cristulata*) is a small eastern Pacific bivalve presently classified in the Cardiniidae, a family otherwise known as fossils from the Paleozoic and early Mesozoic. Evidence from shell characters including external sculpture, hinge teeth, and adductor muscle scars suggests a more appropriate placement in the subfamily Myrteinae of Lucinidae. This is the first record of a myrteine in the eastern Pacific.

Additional keywords: Bivalvia, Myrteinae

INTRODUCTION

The marine bivalve genus *Tellidorella* Berry, 1963 includes a single, small (ca. 6 mm) living species, *T. cristulata* Berry, 1963, which ranges from Baja California to Peru on the eastern Pacific at offshore shelf depths. The familial classification of the genus has been problematic. Originally placed in the Crassatellidae by Berry (1963) it was moved to the Cardiniidae by Cox and Chavan (1969) and regarded as a living species of a family that otherwise ranged from the Ordovician to early Jurassic periods (in their words, a 'living fossil'). In the meantime, from Pliocene beds of Ecuador, Olsson (1964) described a new genus, *Lirotarte*, with *L. paphia* Olsson, 1964 as type species, which he placed in the Astartidae. This species closely resembles *T. cristulata* and the new genus was subsequently synonymized with *Tellidorella* by Cox and Chavan (1969). They provided the first illustration of *T. cristulata* with an outline drawing of the shell interior and photographic images of *Lirotarte paphia*. Since then *Tellidorella* has continued to be classified within the Cardiniidae (Keen, 1971; Dockery, 1982; Bernard, 1983). However, we believe that *Tellidorella* is much better placed in the chemosymbiotic family Lucinidae rather than Cardiniidae, Crassatellidae or Astartidae and we outline our reasons below with new figures and analysis of characters.

SYSTEMATICS

Tellidorella Berry, 1963

Type Species: *Tellidorella cristulata* Berry, 1963:140, by monotypy.

Lirotarte Olsson, 1964: 40. Type species: *L. paphia* Olsson, 1964: 40, pl. 5, figs. 8, 8a–f), Pliocene, Ecuador, Esmeraldas Formation. Length 3.2 mm, height 3 mm.

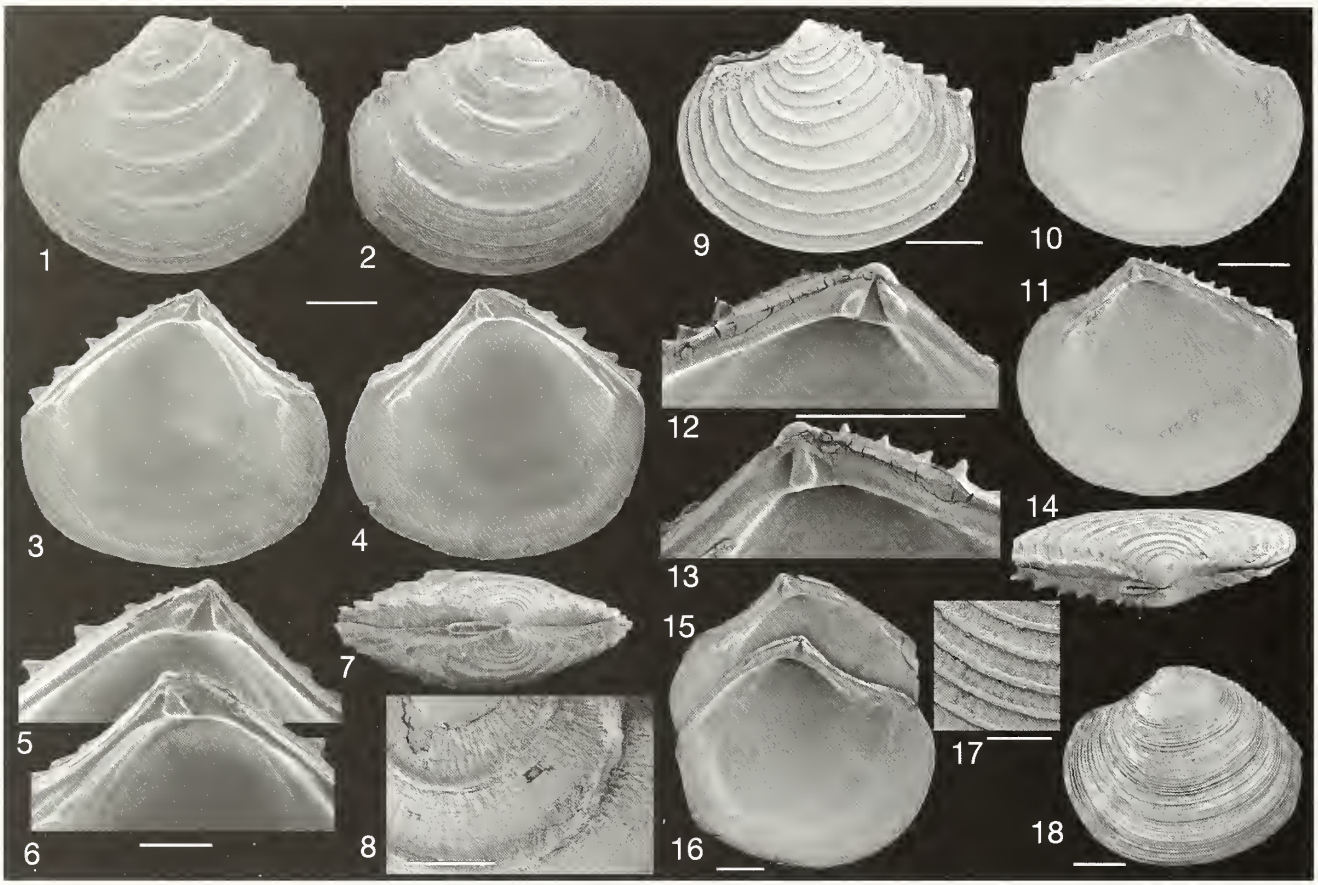
Description: Shell features as for *T. cristulata* below.

Remarks: Berry (1963) suggested placement of *Tellidorella* in Crassatellidae because of a general similarity with *Crassinella* species but noting (p. 140) that the hinge ". . .is altogether distinctive if not indeed unique." A year later, Olsson (1964) placed *Lirotarte* in Astartidae. Cox and Chavan (1969) synonymized the two genera and placed *Tellidorella* in the Cardiniidae, stating (p. N580) "This small shell is a 'living fossil' having all morphological characters of the Cardiniidae, among which are the right duplicate, V-shaped posterior laterals, lack of distinct *5b*, a long *A1*, no marginal *A1V* and *P1V*."

Tellidorella cristulata Berry, 1963
(Figures 1–8, 19)

T. cristulata Berry, 1963: 140
T. cristulata.— Cox and Chavan, 1969: N580, fig. E80A2 (figs. E80A1a–c are *T. paphia* (Olsson, 1964))
T. cristulata. —Keen, 1971: 106 fig. 236 (right valve, interior and exterior of holotype.)

Description: Shell very small (length ca. 6 mm), laterally compressed, slightly asymmetrical with left valve slightly smaller, subtrigonal, ventrally rounded, posteriorly slightly truncate, umbones prominent, sharp, moderately prosogyrate. Sculpture of around 10 widely spaced, projecting commarginal lamellae that become bluntly spinose along the posterodorsal margin. Posterior dorsal area with lower commarginal lamellae in many specimens. Interspaces between commarginal lamellae



Figures 1–8. *Tellidorella cristulata* Berry, 1963, dredged, SE of Punta San Antonio, Sonora, Mexico, 27°53′60″ N, 111°4′32″ W. Santa Barbara Museum of Natural History, SBMNH 83203. **1–2.** Exterior of left valve (**1**) and right valves (**2**). Scale bar = 1 mm. **3–4.** Interior of left and right valves. **5–6.** Detail of cardinal teeth in left (**5**) and right (**6**) valves. Scale bar = 0.5 mm. **7.** Dorsal view showing lunule, ligament and escutcheon. **8.** Detail of exterior shell sculpture showing radial folds between the commarginal lamellae. Scale bar = 0.5 mm. **Figures 9–18.** *Myrtea spinifera* (Montagu, 1803) (**9–14, 18**) Porcupine Expedition, West of Ireland (Natural History Museum, London, 1885.11.5 817–22) and *Notomyrtea botanica* (**15–17**) New South Wales, Australia, 1.6 km E of Malabar Outlet, Sydney, 66 m (Australian Museum, Sydney, AMS C.360780). **9.** *Myrtea spinifera* juvenile, exterior of left valve. Scale bar = 1 mm. **10–11.** *M. spinifera* interior of left valve (**10**) and right valve (**11**). Scale bar = 1 mm. **12–13.** *M. spinifera*, details of cardinal teeth in left valve (**12**) and right valve (**13**) Scale bar = 1 mm. **14.** *M. spinifera*, dorsal view. **15–16.** *Notomyrtea botanica* interior of right (**15**) and left (**16**) valves. Scale bar = 1 mm. **17.** *N. botanica* detail of external sculpture. Scale bar = 0.5 mm. **18.** *Myrtea spinifera* adult shell. Scale bar = 5mm.

with irregular radial ridges. Lunule lanceolate, elongate, asymmetrical with left side narrower and fitting inside of right valve. Escutcheon long, deep. Ligament external, short. Hinge teeth: right valve with a single triangular cardinal tooth, an elongate anterior lateral tooth and a shorter posterior lateral. Left valve with two small cardinal teeth separated by a triangular socket, anterior and posterior lateral teeth small indentations. Adductor muscle scars unequal, anterior scar larger than posterior. Anterior scar reniform and ventrally detached from the pallial line for about 1/3 of length (Figure 19). Pallial line entire, narrow. Inner shell margin smooth.

Holotype: California Academy of Sciences CAS-IZ 43974.00

Type Locality: Off Puerto Libertad, Sonora, Mexico, 29°51.8′ N, 112°46.8′ W, 73 m.

Relationships of *Tellidorella*: Although *Tellidorella cristulata* is a little studied species, since Cox and Chavan (1969) its familial position has been firmly entrenched in the Cardiniidae. This family, usually assigned to superfamily Crassatelloidea, is known from fossils ranging from the Ordovician to the Lower Jurassic, with eight included genera. No younger representatives are known except for the Cox and Chavan (1969) assignment of *Tellidorella*. Species of *Cardinia* are common in the early Jurassic (Lias) beds of northern Europe and Palmer (1975) provides good illustrations of a diversity of species. *Cardinia* species usually have robust shells with heavy commarginal ridges and often a V-shaped configuration of the heavy lateral teeth but cardinal teeth are usually weak or absent.

The assignment of *Tellidorella* to Cardinidae was made on the superficial similarity of hinge teeth with

the V-shaped posterior lateral teeth of cardinids, supposedly also present in *Tellidorella*. But the V-shaped posterior laterals of *Tellidorella* actually consist of a single lateral tooth that becomes dorsally near-confluent with the edge of the escuteheon. The dorsal limb of the V-shaped laterals is actually the inner edge of the escuteheon. Similarly, the so-ealled duplicate anterior lateral teeth of the right valve are a single, long, true lateral tooth with, dorsally, a groove and then the sharp edge of the lunule. Because the valves of myrteineid lueinids are asymmetrical, the edges of the lunule and eseuteheon of the left valve fit into corresponding grooves of the right valve. The figure of *Tellidorella eristulata* in Cox and Chavan (1969, fig. 80A2) is a misleading drawing that shows apparent V-shaped posterior lateral teeth.

An initial inspection of *Tellidorella cristulata* suggested to us that it would be better classified in the family Lueinidae, with particular resemblance to *Myrtea* species, although *T. cristulata* is smaller than most of these. Aceordingly, we prepared for SEM (scanning electron mieroscopy) examination speeimens of *Myrtea spinifera* (Montagu, 1803), the type species of *Myrtea* Turton, 1822, and *Notomyrtea botaniea* (Hedley, 1918) of similar sizes to *T. eristulata* in order to compare shell eharacters. These *M. spinifera* and *N. botaniea* are juvenile shells, the speeies reaeh 25–30 mm and 15 mm in length as adults, much larger than *Tellidorella*.

Shells of juvenile *Myrtea spinifera* and *Notomyrtea botanica* (Figures 9–18) are strikingly similar to *Tellidorella*. Externally, the shell sculpture of *M. spinifera* eonsists of widely spaced commarginal lamellae that are projeeted into blunt spines along the posterior dorsal margin. The posterior dorsal area is marked by a zone of lower lamellae. The lunule is long, laneeolate and asymmetrieal, the left valve fitting into the right. The escutcheon is long and the ligament short and external. Internally, the hinge teeth are very similar to *Tellidorella*, with a single triangular tooth in the right valve and two small cardinals in the left valve. Lateral teeth are elongate and more prominent in the right valve. The anterior adductor sear has a short length of ventral detachment from the pallial line and the ventral shell margin is smooth. Shell shape and hinge teeth also elosely resemble *Notomyrtea botaniea* (Figures 15–16) from southern Australia. *Myrtea spinifera* laeks any radial seulpture between the commarginal lamellae but this occurs in other *Myrtea* group lucinids such as *Notomyrtea* (Figure 17) and *Eulopia* Dall, 1901 (see Bretsky, 1976: pl. 34, figs. 11–13; Mikkelsen and Bieler, p. 236).

An important group of shell eharacters used in the recognition of Lucinidae coneern the shape and length of the anterior adductor muscle scar. In most lucinids this is ventrally detached from the pallial line and extends as an inwardly directed lobe. The muscle scar varies both in length and in the angle of and extent of ventral detachment from the pallial line. In genera such as *Miltha* and *Lueinoma* the scar is very long and extensively detached, while in others such as *Myrtea* and

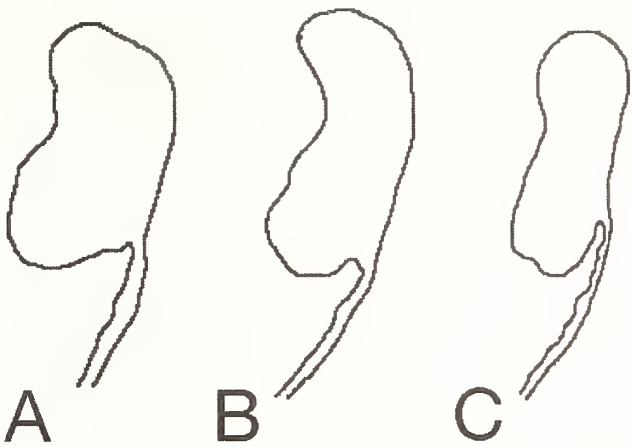


Figure 19. Tracings of anterior adductor muscle scars in left valve. **A.** *Tellidorella cristulata*, **B.** *Myrtea spinifera*, **C.** *Notomyrtea botanica*. Not to scale.

Parvilueina, it is short and only slightly detached from the pallial line. Images of *Tellidorella eristulata* clearly show the anterior adductor scar with a short ventral detachment from the pallial line (Figure 19). This is similar to *Myrtea spinifera* and other '*Myrtea*' group lueinids (e.g., Glover and Taylor, 2007: fig. 6; Cosel and Bouchet, 2008: fig. 14). *Tellidorella* shells also have brown staining on the shell located at positions of the anterior inhalant and posterior exhalant tubes indicating the anterior–posterior water flow typical of lucinids. Moreover, a body reconstituted from a dried shell possessed ctenidia with single demibranchs only and a narrow, elongate foot typical of Lucinidae.

In summary, the similarity of shell characters between *T. eristulata* and juvenile *Myrtea spinifera* and *N. botanica* indieate a elose relationship. These include the laterally compressed shells, lateral asymmetry, the widely spaced commarginal lamellae projected into posterodorsal flutes, the long lanceolate lunule, the short external ligament, the similar arrangement of cardinal teeth and the elongate lateral teeth more prominent in the right valve and the anterior adductor muscle with a short length of ventral detachment from the pallial line. *Tellidorella* speeimens are always about 6 mm in length and we conclude that it is a small species. Despite the similarity of *Tellidorella* to juveniles of *Myrtea* and *Notomyrtea*, adults of these genera are morphologically distinct (Figure 18).

Although no suitably preserved material was available for moleeular analysis we are confident that the shell characters of *Tellidorella cristulata* indicate placement in the Myrteinae subfamily of the Lueinidae. The Myrteinae was first proposed as a subfamily by Chavan (1969) but he included some genera such as *Lucinoma* and *Monitilora* that recent molecular analyses exclude, although speeies of *Myrtea*, *Notomyrtea* and *Gloverina* form a highly supported clade distinct from all other lueinids (Taylor et al., in press). Little is known of the biology of most myrteines but *Myrtea spinifera* lives in

offshore muds in the north-western Atlantic and, in common with all studied Lucinidae (Taylor and Glover, 2000), possesses symbiotic sulphide-oxidizing bacteria housed in bacteriocytes of the ctenidia (Southward, 1986; Dando et al., 1985). Recent deeper water sampling in the tropical Indo-West Pacific has recovered a diversity of species within the subfamily (Glover and Taylor, 2007; Cosel and Bouchet, 2008).

As well as *Tellidorella paphia* (Olsson, 1964), from the Pliocene of Ecuador, another fossil that can be assigned to the genus is the early Oligocene species *Tellidorella interlacinia* Dockery, 1982: pl. 20, figs. 9–10) from the Vicksburg Group, Mississippi, USA, 6.5 mm length. Interestingly, although Dockery classified *Tellidorella* in Cardiniidae he placed the figure amongst Lucinidae species on plate 20. Also, Squires (1990) pointed out that *Corbis inclellani* Hanna, 1927 (length 6 mm) from the middle Eocene of southern California is a likely *Tellidorella* species.

Our conclusion is that *Tellidorella* is not a "living fossil" member of the otherwise Paleozoic–early Mesozoic family Cardiniidae, but should be classified as a small, distinctive eastern Pacific genus in the Myrteinae subfamily of Lucinidae. Although 32 species of Lucinidae are known from the temperate and tropical eastern Pacific (Coan, Valentich-Scott, and Bernard 2000; Coan and Valentich-Scott, in preparation), *Tellidorella* is the only member of the Myrteinae yet recorded.

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A new gigantic species of *Zeidora* Adams, 1860 from Antarctic waters (Gastropoda: Fissurellidae)

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ABSTRACT

A new species of *Zeidora*, *Z. antarctica* new species, is described from Bellingshausen Sea, Antarctica. The species is characterized by having a large and low shell, with delicate shell sculpture, spire extending beyond the shell's outline, and relatively wide septum, curved at the anterior margin.

Additional keywords: Bellingshausen Sea, Southern Ocean

INTRODUCTION

To date, 14 Recent species of *Zeidora* are known around the world, most of them remaining poorly known and based only on shell morphology (Geiger, 2006). Of these species, eight are known from the northern hemisphere, in the Caribbean (*Zeidora naufraga* Watson, 1883; *Z. bigelowi* Pérez-Farfante, 1947; *Z. neritica* Espinosa, Ortea, and Fernández-Garcés, 2004; and *Z. milerai* Espinosa, Ortea, and Fernández-Garcés, 2004), Japan (*Z. calceolina* A. Adams, 1860; *Z. reticulata* A. Adams, 1862), Panama [*Z. flabellum* (Dall, 1896)], and the Red Sea [*Z. nesta* (Pilsbry, 1890)]; and six species from the southern hemisphere, from Galapagos Islands [*Z. galapagensis* (McLean, 1970)], Easter Island (*Z. balhamondei* Rehder, 1980), Australia [*Z. lodderae* (Tate and May, 1900), *Z. legrandi* Tate, 1894, and *Z. tasmanica* (Beddome, 1883)], and New Zealand (*Z. maoria* Powell, 1936). Tate and May (1901) regarded *Zeidora legrandi* as a junior synonym of *Z. tasmanica*; and Kuroda et al. (1971) and Kilburn (1978) reported *Z. reticulata* as a synonym of *Z. calceolina*, although this opinion was not shared by Herbert (1987).

In this paper, a new species of *Zeidora* from the Bellingshausen Sea, Antaretiea, is deseribed. The material reported here was collected during the BENTART Expedition (Spanish Antarctie Program) aboard the R/V Hespérides, using an Agassiz trawl; and was deposited at the Museo de Historia Natural de Madrid (MNCN), Spain. For eomparative purposes the eollection of The Natural History Museum (NHMUK), London was studied, examining the types of *Zeidora naufraga* Watson, 1883 (holotype: NHMUK 1887.2.9.128), *Z. maoria* Powell, 1936 (2 syntypes: NHMUK 1962954/1-2), and *Z. reticulata* A. Adams, 1862 (holotype and another speeimen: NHMUK 1878.1.28.150).

SYSTEMATICS

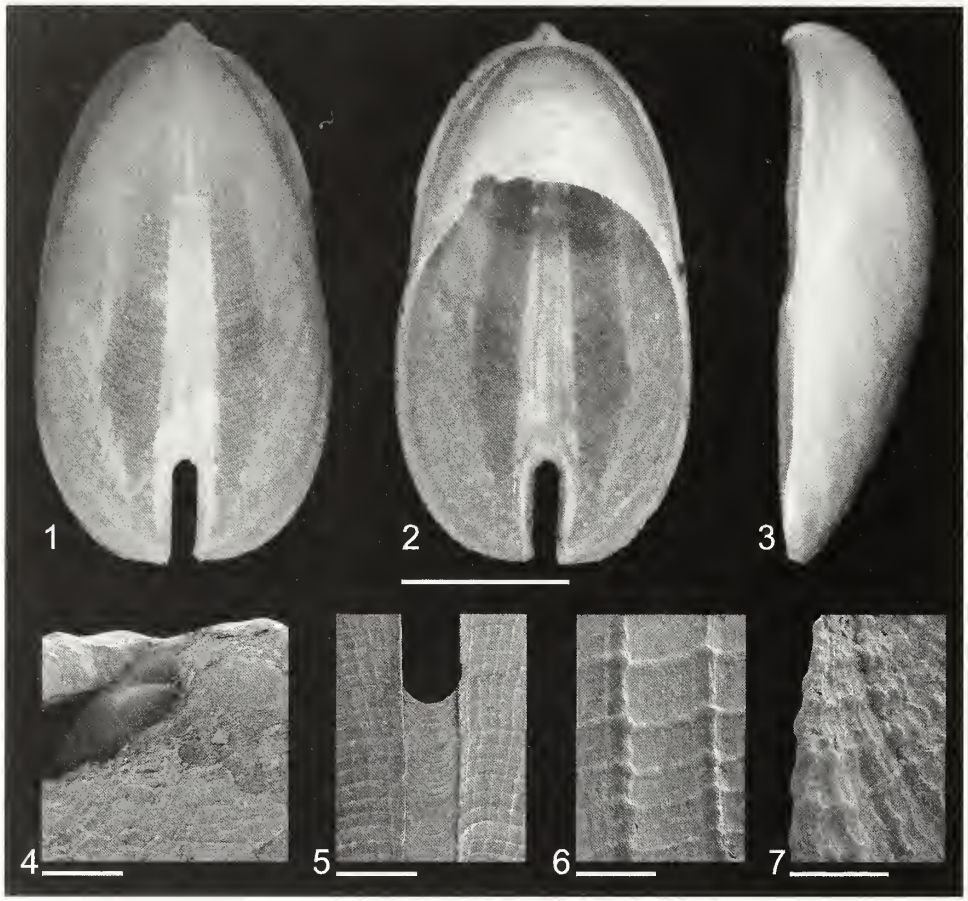
Family Fissurellidae Fleming, 1822
Genus *Zeidora* A. Adams, 1860

Type Species: *Zeidora calceolina* A. Adams, 1860 (by monotypy)

Zeidora antarctica new species
(Figures 1–8)

Diagnosis: Shell large, ovately elongated, low; spire posteriorly loeated, extending beyond shell's outline. Shell surface with delieate reticulate seulpture. Septum relatively wide, one-fourth total shell length, with anterior margin markedly curved.

Description: Shell large (16.2 mm length in the holotype), with high expansion whorl rate, whitish, delicate, translueent. Spire of 1¼ whorls, located on posteroventral margin, extending beyond shell outline. Protoconch of one whorl, 150 µm in diameter, planorboid,



Figures 1–7. Holotype of *Zeidora antarctica* new species (MNCN 15.05/53569). **1.** Dorsal view. **2.** Ventral view. **3.** Lateral view. **4.** Protoconch. **5.** Selenizone and slit. **6.** Detail of shell sculpture. **7.** Crenulations of postero-ventral margin. Scale bars: Figures 1–3 = 5 mm; 4 = 100 µm; 5 = 1 mm; 6 = 200 µm; 7 = 500 µm.

slightly twisted to right (Figure 4). Last whorl strongly elongated, ovate, narrow in outline (width / length ratio = 0.55), low (height / length ratio = 0.29) (Figures 1–3). Base with widely curved lateral margins; posterior margin short, almost straight; anterior margin gently curved (Figure 2). Selenizone extending along entire teleoconch whorl, relatively wide, sculptured with distinct commarginal ribs, surrounded by narrow keels (Figures 1, 5). Slit open, with margins parallel, wide and short (1/5 total shell length). Shell surface sculptured with about 80 primary radial ribs, crossed by ~100, almost equally developed, commarginal ribs. Intersection of radial and commarginal ribs producing small nodules and squarish interspaces (Figure 6). Between primary ribs, microscopic (secondary) radial and commarginal threads (Figure 6). Primary radial ribs producing small crenulations at postero-ventral margin (Figure 7). Inner shell surface whitish and brilliant, outer shell sculpture showing through. Internal septum relatively large, extending for about 1/4 total shell length, with markedly curved anterior margin.

Type Locality: 70°8′12″ S, 84° 51′ 41″ W, Bellingshausen Sea, Antarctica, 603 m (Figure 8).

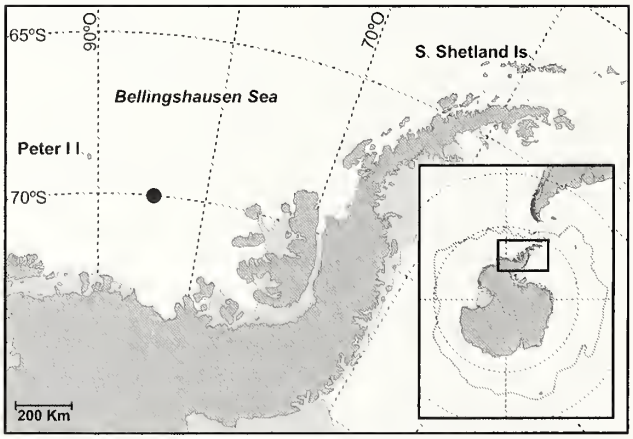


Figure 8. Location map showing the type locality of *Zeidora antarctica* new species (•).

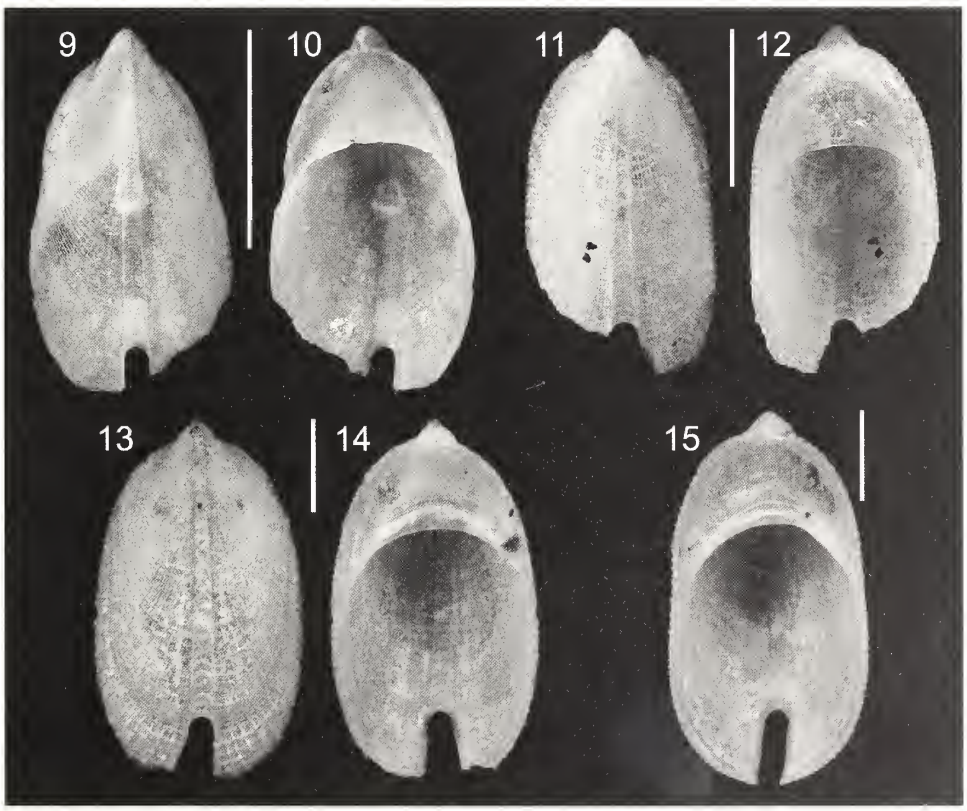
Type Material: Holotype, MNCN 15.05/53569; measurements in Table 1.

Distribution: Only known from the type locality.

Table 1. Living species of *Zeidora*. Providences and measurements (L, length; W, width; H, height) of their types (h = holotype; p = paratypes).

Species	Type locality	Depth (m)	Measurements (L × W × H, in mm)
Z. antarctica new species	Bellingshausen Sea, Antarctica	603	16.2 × 8.9 × 4.7 (h)
Z. bahamondei Rehder, 1980	Vaihu, Easter Island	?	5.2 × 3.1 × 1.3 (h)
			4.2 × 2.9 × 1.2 (p)
Z. bigelowi Pérez-Farfante, 1947	Cochinos Bay, Cuba	320-412	2.5 × 1.5 × 1.0 (h)
Z. calceolina A. Adams, 1860	Straits of Korea, Japan	115	4.0 × ? × ? (h)
Z. flabellum (Dall, 1896)	Off Clarion Island, Lower California	841	10.0 × ? × 2.5 (h)
Z. galapagensis (McLean, 1970)	Isla Isabela, Galapagos	146-183	5.5 × 3.3 × 1.7 (h)
Z. lodderae (Tate and May, 1900)	Tasmania	?	10.0 × 6.4 × 2.8 (h)
Z. maoria Powell, 1936	Off Three King Island, New Zealand	260	2.9 × 1.4 × 0.9 (h)
Z. milerai Espinosa, Ortea and Fernández-Garcés, 2004	Rancho Luna Beach, Cienfuegos, Cuba	28	3.5 × 2.1 × 1.4 (h)
Z. naufraga Watson, 1883	North of Culebra Island	713	9.7 × 5.1 × 3.0 (h)
Z. neritica Espinosa, Ortea and Fernández-Garcés, 2004	Vista del Mar Beach, Habana, Cuba	18	2.5 × 1.6 × 0.9 (h)
Z. nesta (Pilsbry, 1890)	Red Sea	?	5.5 × 3.0 × 1.3 (h)
Z. reticulata A. Adams, 1862	Mino-Sima, Japan	?	4.0 × 2.4 × ? ([1])
			4.2 × 2.3 × ? ([1])
Z. tasmanica (Beddome, 1883)	Kelso Bay, Tasmania	31	5.0 × 3.0 × 0.8 (h)

([1]) A single vial containing two specimens of *Z. reticulata* is housed at the NHMUK. One of these specimens is the holotype, and the other -coming from Cuming collection- it is not a type; however, there is no way of knowing which specimen is which.



Figures 9–15. *Zeidora* species. **9-10.** Holotype of *Z. naufraga* (NHMUK 1887.2.9.128). **11-12.** Paratype of *Z. maoria* (NHMUK 1962954). **13-15.** Holotype and another specimen of *Z. reticulata* (NHMUK 1878.1.28.150). Scale bars: Figures 9–10 = 5 mm, 11–15 = 1 mm.

Etymology: The species is named after the geographic area where the specimen was collected.

Remarks: *Zeidora antarctica* new species closely resembles Z. *naufraga* (Figures 9–10), Z. *maoria* (Figures 11–12), and Z. *reticulata* (Figures 13–15) in general shell outline and sculpture. However, in these species the spire is larger and more markedly extending past the posterior margin of shell, even when these specimens are smaller in size. In addition, Z. *naufraga* and Z. *maoria* have a less concave anterior margin of septum than Z. *antarctica*; Z. *naufraga* has a shorter and wider slit; and Z. *reticulata* has a larger posterior margin and stronger keels surrounding the selenizone. Furthermore, the shell sculpture in Z. *maoria* and Z. *reticulata* produces rectangular interspaces, while in Z. *antarctica* interspaces are squarish.

Regarding the other living species of the genus, *Zeidora antarctica* differs from Z. *balhamondei*, Z. *lodderae*, and Z. *tasmanica* by having a longer and narrower shell outline; from Z. *calceolina* by having delicate shell sculpture; and from Z. *nesta*, Z. *flabellum*, Z. *galapagensis*, Z. *balhamondei*, Z. *milerai*, Z. *neritica*, and Z. *bigelowi* by having a wider septum. Z. *antarctica* also is distinguished from any other species by its extremely large size and allopatric geographical distribution (Table 1), since the new species described here provides the first record for the genus in Antarctic waters.

Thiele (1929) divided *Zeidora* in two subgenera: *Zeidora* sensu stricto and *Nesta* H. Adams, 1870, a criterion subsequently followed by Wenz (1938), Keen (1960), and Herbert (1987). The presence of a broad septum in *Zeidora antarctica*, clearly placed this species in the nominotypic subgenus.

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Do *Philomycus carolinianus* (Gastropoda: Philomycidae) prefer to congregate?

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ABSTRACT

Field observations of land slugs *Philomycus carolinianus* (Bosc, 1802) together at shelters led us to ask whether they were attracted to conspecifics versus attracted to a limited resource (e.g., shelter). Our laboratory experiment offered three shelters to three slugs in each replicate, with the expectation that slugs would occur together under a single shelter if they preferred to be with conspecifics, while slugs would occur singly under each shelter if they avoided conspecifics. We found that slugs chose shelters regardless of the presence of conspecifics, suggesting that their occurrence together in nature is due to the sharing of limited shelter resources.

Additional key words: land slugs, shelter, limited resource

INTRODUCTION

Animals congregate for many reasons. In some cases, they benefit from the presence of others. In other cases, they occur together in an area because a resource is present there. Explanations for congregation behavior in terrestrial mollusks include prevention of water loss (Dundee et al., 1975; Cook, 1981; Waite, 1988) and escape from ground-level heat (Cook, 2001).

In nature, gastropods are commonly associated with woody debris, and can be found congregated in areas with large amounts of such debris (Kappes et al., 2009). Individuals of species of slugs in the genus *Philomycus* Rafinesque, 1820 are sometimes seen in close proximity to each other, especially near coarse woody debris. In some cases, these slugs are found in physical contact with each other (a phenomenon known as huddling). However, *Philomycus* individuals do not always exhibit huddling in the wild, and the presence of multiple slugs in close proximity is yet to be explained. Two possible explanations are that individuals of *Philomycus* species are gregarious (prefer to associate with each other) and that they tend to congregate at the locations of limiting resources, regardless of the presence of other slugs.

Huddling and congregation are not unique to *Philomycus* species. Örstan (2007) noted huddling by individuals of the same and of different species of slugs, but we do not know whether the same mechanisms are acting in inter- and intra-specific huddles. In addition, although we now have better understanding of the systematics of Philomycidae (Fairbanks, 1986; 1989; 1990; 1993; 1998; Tsai et al., 2005; Tsai and Wu, 2008), we still know relatively little about their biology. In this note, we examine congregation and huddling behavior among individuals of a single species, the eastern North American slug *Philomycus carolinianus* (Bosc, 1802).

MATERIALS AND METHODS

Slugs were wild-caught in spring 2009 from the Patuxent National Wildlife Refuge, Prince George's County, Maryland (39°03′ N, 76°49′ W). The slugs were used in another experiment over the summer, then provided to us for this study, which was conducted from 27 October to 21 November 2009. Voucher specimens, preserved in 80% EtOH within a day post mortem, are deposited at Carnegie Museum of Natural History (CM104587).

We prepared three arenas. Each was 44 × 28 × 22.5 cm high. The arenas were corrugated cardboard boxes, each lined with a plastic bag and covered with a 1.4 mm mesh screen. To maintain humidity in the arenas, each screen was covered with a stack of 12 moistened paper towels. Each paper towel had a surface area of 276 cm^2. Each arena floor was covered with soil approximately 1 cm deep. In each arena, we placed three bark shelters measuring approximately 12 cm long, 10 cm wide, and 1.5 cm thick. Each arena also contained a water dish and a food dish that contained fish food flakes and mushroom slices. The amounts of food and water provided were ample for the number of slugs in each arena, ensuring that neither food nor moisture was limiting. Shelter was the limiting factor; other than the bark, food dish, and water dish, the arena was devoid of objects that could function as shelters.

We placed three mature slugs in each arena. For each replicate, we observed slug positions once daily for six days. Observations were made during the daytime when slugs would more likely be resting under shelters. Time of day when observations were made ranged from 7:42–21:44 with a mean of 12:55 (95%, CI 9:00–16:50). Because we had a limited number of slugs, we re-used slugs in subsequent trials to maximize the number of replicates. The assigning of individuals to arenas was not strictly random. Rather, with the exception of 2 individuals in the last trial, the slugs were grouped in a manner ensuring that the individuals together in one trial would not be together in a subsequent trial.

We compared the observed slug positions with a null model, which assumed a random distribution of slugs under the shelters. We generated the null model by determining the 18 possible arrangements of three slugs under three shelters. This null model predicts nine instances of singletons (slugs alone under shelters), six instances of pairs (two slugs under the same shelter), and three instances of triplets (three slugs under the same shelter). Triplets would be expected to be more common if slugs are gregarious and less common if they prefer to be solitary. We used a chi-square test to determine the statistical significance of the observations.

RESULTS AND DISCUSSION

Table 1 shows the observed and expected numbers of shelters with different numbers of slugs. With eight replicates (a total of 83 observations), we observed 46 instances of slugs alone under shelters, 31 instances of two slugs under the same shelter, and six instances of three slugs under the same shelter. We discarded 18 observations in which at least one slug was not under a shelter or in which a slug was using the food or water dish as a shelter. We also discarded two replicates in which one of the slugs died. The observed and expected values are not significantly different from random (χ^2 = 5.33, 2 degrees of freedom, $0.1>P>0.05$).

This result suggests that slugs choose shelters randomly, without regard to whether another slug is present. Of particular interest is the observed trend for fewer triplets than predicted by the random model (6 vs. 13.8). Although this trend is not statistically significant, it does suggest that these slugs are not gregarious.

Table 1. Number of shelters having 1, 2, or 3 slugs underneath. χ^2 analysis indicates the slugs were behaving randomly ($0.1>P>0.05$).

Number of slugs in shelter	Observed	Expected	χ^2_p
1	46	41.5	0.49
2	31	27.7	0.40
3	6	13.8	4.44
Totals	**83**	**83**	**5.33**

Because these slugs appear to assort randomly, congregations of slugs found in nature may indicate the presence of a scarce resource (e.g., shelter) in that particular location. Therefore, observations of slug huddling could be used as evidence for resource scarcity. For example, some land slugs appear to cluster to conserve moisture (Dundee et al., 1975; Cook, 1981; Waite, 1988; although see Welsford et al., 1990). In this experiment, food and moisture were non-limiting. A repetition of the experiment in which moisture, rather than shelter, was the limiting factor might allow us to study whether individuals of *Philomycus carolinianus* do huddle to conserve moisture. Investigations in which other resources were limiting could also address whether huddling occurs due to the scarcity of other resources.

All of the slugs used in this investigation were mature. An investigation of the effects of age on congregation behavior could provide additional data on the behavior of *Philomycus* species. Studies involving species other than *P. carolinianus* could determine whether other species show similar behaviors.

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Authorship and date of a key South American paper by Phillip P. King (1832)

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ABSTRACT

An important paper describing many species of new marine and terrestrial mollusks from southern South America was published in the early 1830s. Its authorship has been attributed either to King and Broderip or to King alone, and its date has been given variously as 1830, 1831, or 1832. We here contend that King alone should be considered its author and that it should be dated as July 1832.

Additional keywords: Patagonia, Tierra del Fuego, malacological literature

INTRODUCTION

At the beginning of the 19th century, a number of expeditions provided the first insights into the knowledge of the fauna from the southern tip of South America and the adjacent Antarctic waters. In this regard, the results of H.M.S. Adventure and Beagle represent a pioneer contribution regarding mollusks, brachiopods, and barnacles. A paper describing material from this expedition was published in the penultimate issue of *The Zoological Journal*, Volume 5, Part 19, pages 332–349. The significance of that paper arises in the descriptions of 67 new species, including 14 species of marine bivalves – one of them the commercially important scallop *Zygochlamys patagonicus*, 24 species of marine gastropods, 2 chitons, 18 terrestrial gastropods, 4 freshwater gastropods, 3 barnacles, and 2 brachiopods. In addition, a new gastropod genus, *Marinula*, was introduced. The title of this non-illustrated paper is:

> "Description of Cirrhipeda, Conchifera and Mollusca, in a collection formed by the officers of H.M.S. Adventure and Beagle employed between the years 1826 and 1830 in surveying the southern coasts of South America, including the Straits of Magalhaens and the coast of Tierra del Fuego. By Captain Phillip P. King, R.N., F.R.S., &c., assisted by W. J. Broderip, Esq. F.R.S., & c."

It will be noted that the "authorship" of this paper was oddly styled, and it has also been assigned various publication dates, both matters addressed here.

AUTHORSHIP

The inclusion of Broderip seems to be an unusually placed acknowledgement, but we have seen similar examples used to emphasize an acknowledgment of a non-author. It is clear from the content of the article that King considered himself to be its author. In the second paragraph of the article, he wrote:

> "In the description of the species I have the benefit of the advice and assistance of my friend Mr. Broderip; and to his knowledge of the subject, and the attention which he has devoted to my collection, I owe in a great measure the paper which I have now the satisfaction of presenting to the public through the medium of the Zoological Journal" [emphasis supplied].

In several other places in the introduction and elsewhere in the article, King referred to the author of the article as "I", and on p. 342, King again referred to "my friend, Mr. Broderip". The running head of the article is "Capt. P. P. King's Description of Cirrhipedia, Conchifera, and Mollusca."

It is notable that when Broderip had reason to refer to the species named in this paper, he always showed King alone as author. For example, in a paper read at the Zoological Society of London on 29 February 1832, Broderip (1832: 27) commented under his description of *Chiton setosus* that "This species is very distinct from *Chit. setiger*, King, (Zool. Journ. vol. v. p. 338) . . ."; and under *C. frembleii*, Broderip (1832: 28) stated differences between it and "*Chit. setiger*, King". In the *Penny Cyclopedia* article on *Helix*, Broderip (1838: 108) mentioned *Marinula* King.

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In addition to Broderip, many other authors attributed the taxa described in this paper to simply "King", among them G. B. Sowerby I (1832), Catlow and Reeve (1845), Agassiz (1848), Carpenter (1857), Iredale (1915), Pfeiffer (1857), Suter (1913), and Thiele (1929).

On the other hand, d'Orbigny (1834–1847), in his *Voyage dans l'Amérique Méridionale*, was inconsistent, crediting some taxa to Broderip and others to King. The frequent usage of "King & Broderip" appears to be a rather recent change in the second half of the 20th century after Sherborn (1922–1933) credited the species to "King & Broderip". Marincovich (1973) used "King" when referring to the genus *Marinula*, but "King & Broderip" in his Literature Cited. Powell (1960) and Dell (1964) used "King" when referring to some species and "King & Broderip" when referring to others. The usage of "King & Broderip" became more common at the end of 20th century, and is often the current usage (Jonkers, 2003; Osorio, 2002; Pastorino, 2005a, b; Pastorino and Harasewyeh, 2000; Reid and Osorio, 2000; Signorelli and Pastorino, 2011; Zelaya, 2005; among many others).

A modern work using the same type of assistance acknowledgment is *The American Museum of Natural History Guide to Shells* by W. K. Emerson and M. K. Jacobson (1976), "with the assistance of Harold S. Feinberg and William E. Old, Jr." The Library of Congress cataloging data has author as William K. Emerson with Morris K. Jacobson as joint author, with Feinberg and Old not mentioned.

Although the *International Code on Zoological Nomenclature*'s Article 50.1 (ICZN, 1999: 52) precludes the use of outside sources to determine authorship, we take the view that attribution to King is inherent in the paper, and that attribution to King by other authors, and especially by Broderip himself, is confirmation of our interpretation of the oddly phrased authorship on the paper. It is therefore our conclusion that King alone should be regarded as author of the paper and of the included taxa.

DATE

The issue of *The Zoological Journal* containing this paper was the penultimate one, and the journal's operation was not smooth. There is no real dating on this part of the volume. The cover of volume 5 is imprinted "From 1832–1834", and the bottom of the cover is dated 1835. The Contents page for Part XIX containing this paper is imprinted "July, 1830.–September, 1831.", which is obviously meaningless. This paper and its contained species have been dated by various authors as 1830, 1831, 1832, and even 1835.

Pilsbry (1911: 525) seems to be the source of the mistaken date of 1830, and this has been followed by some subsequent authors. A footnote in the King paper itself (p. 341) notes that, while the paper was being printed, the September 1831 issue of the *Annales des Sciences Naturelles* had arrived describing one of the new species, and the type was then altered to accommodate the footnote and to change the species name footnoted. The paper could not thus have appeared until after September 1831.

Evidently, proofs of this paper were made available to some workers soon after September 1831. For example, the barnacle *Elminius leachii* described on page 334 was figured by G. B. Sowerby I in a work that appeared on 4 January 1832. Sowerby (1832: unnumbered) stated that "Capt. King has named the species *Elminius leachii*, see Zool. Journ. vol. V. p. 334." There is a footnote on page 334 of the *Zoological Journal* article stating that the species had already been named *Elminius kingii* Gray, perhaps too late for the text to be changed, a fact not noted by Sowerby. As noted above, Broderip cited two of King's chitons in a meeting in February 1832.

For unknown reasons, this issue was withheld and not distributed to subscribers until July 1832. In a review published in November 1832, N. A. Vigors, the editor, noted that it was "published in July last" along with some supplementary plates. This is the date given, without explanation, by Sherborn (1922–1933) in his entries for the included species. Most subsequent authors have followed this (e.g., Jonkers, 2003; Pastorino 2005a, b; Pastorino and Harasewych, 2000; Reid and Osorio, 2000; Signorelli and Pastorino, 2011; Zelaya, 2005; among others).

This paper was evidently King's only contribution to malacology. He published a number of articles on vertebrates, geography, and meteorology. Most of his material from this key invertebrate paper is in The Natural History Museum in London.

CONCLUSIONS

The authorship of the paper often cited as of "King & Broderip," is attributable to only P. P. King as are the taxa described therein. The date of the paper should be cited as July 1832.

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Species of *Anatoma* (Gastropoda: Anatomidae) in Norwegian and adjacent waters, with the description of two new species

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ABSTRACT

The species of *Anatoma* Woodward, 1859 from Norwegian waters and from the Norwegian Sea are treated taxonomically. *Anatoma crispata* (Fleming, 1828) has until quite recently been regarded as the sole representative of this family in north European waters, but constant conchological differences make it evident that at least three species have been lumped under this name in Norwegian and other Scandinavian literature. Three species, *A. crispata, A. aspera* (Philippi, 1844) and *A. tenuisculpta* (Seguenza, 1877) are redescribed and two new species from deep water in the Norwegian Sea, *A. schioettei* new species and *A. schanderi* new species, are described based on shell characters. The distribution in inshore Norwegian waters and in the Norwegian Sea is described, and possible microhabitats suggested. Also geographical variability of conchological characters is discussed in some detail.

Additional keywords: Mollusca, Scissurelloidea, Vetigastropoda, Norwegian inshore waters, bathyal, Norwegian Sea

INTRODUCTION

Until recently it has been universally accepted that the family Anatomidae is represented in north European waters by a single species, *Anatoma crispata* (Fleming, 1828). In a paper, in which also *A. crispata* was recorded from Bergen, Lovén (1846) described, but did not illustrate, *Scissurella angulata*, from northern Norway. Except for Lovén, no one has questioned that *A. crispata* is the only species of the family in Norway, although several authors remarked that two or more varieties might be present. All early authors (e.g. Friele, 1874 and Verkrüzen, 1875), reported *A. crispata* without further discussion. However, Jeffreys (1870) and G.O. Sars (1878), remarked that the specimens found in Norway might be a larger variety of the British form, and G.O. Sars mentioned *A. aspera* and *A. angulata* as synonyms. Odhner (1912) is the first author to clearly distinguish between three varieties of *A. crispata* in northern waters: *A. crispata* sensu stricto, *A. crispata* "var. *angulata*" Lovén, 1846, and *A. crispata* "var. *aspera*," (= var. *paucicostata* Jeffreys, 1865) all of which he recorded from Norwegian waters, but without any clear differentiation of geographic localities.

Recently, Warén (in Hansson 2003) stated that both *A. aspera* and *A. crispata* are found in western Norway, and that there is a possibility that a third species is present in western Sweden and in northern Norway as well.

For several decades, one of us (T.H.) accumulated a sizeable material of *Anatoma* from the coast of Norway. This material, in addition to material graciously donated to T.H. (now deposited at ZMBN) by Per Bie Wikander, material from the H2Deep project, and available museum lots, has made it possible to reassess the genus in Norwegian waters and the Norwegian Sea. Constant conchological differences make it evident that at least three species have been lumped as *Anatoma crispata* in Norwegian and other Scandinavian literature. In this article, we designate **neotypes** and redescribe *A. crispata* and *A. aspera* based on material from the western Mediterranean, the north Atlantic, the Norwegian Sea and Norway. Additionally we resurrect and redescribe *A. tenuisculpta* (Seguenza, 1877) based on material from the western Mediterranean and the northeastern Atlantic Ocean. Furthermore, we describe two new species: *A. schioettei* new species, based on material from the shelf off East Greenland (75° N) and a hot vent locality northeast of Jan Mayen, and *A. schanderi* new species, from the bathyal and abyssal of the Norwegian Sea. Finally, the distribution of the three species in inshore Norwegian waters is discussed. Since *A. crispata* is the type species for the genus *Anatoma* in the family Anatomidae, it is of particular importance to unravel the taxonomic problems associated with this species, which has been misunderstood for such a long time.

MATERIALS AND METHODS

The geographic area covered is primarily the coast of Norway, but the availability of additional material from various parts of the Norwegian Sea (in this context used as a collective for the Norwegian Sea proper, the Iceland

Sea and the Greenland Sea) allowed for the inclusion of the entire area between Norway and Greenland as well. The study is based on material from five summer cruises along the Norwegian coast in the period 1967 to 1971. These cruises covered most of the coast from the Russian border to Stadt (70°15′ N to 62° N), and resulted in 164 specimens and 546 empty shells of species of *Anatoma*. In addition, Per Bie Wikander had collected 163 specimens (plus 20 empty shells) in the Skagerrak and Bodø regions, in the southern and northern part of Norway respectively. Seventy-four specimens and 26 shells were collected at various times between 1965 and 2010 near the Biological Stations of the University of Bergen. A few samples from the upper slope collected by Torleiv Brattegard (Høisæter, 2010) that contained specimens of *Anatoma* are included as well. A few specimens from the MAREANO program, and three small, but most interesting samples from ROV-assisted sampling of hot vents and other deep-water localities around Jan Mayen, during the H2DEEP program contributed to expand the geographic and bathymetric coverage. The scope of the investigation was further enhanced by museum material from Hamburg (ZMH) and Copenhagen (ZMUC) examined. In addition all material from the four university-based museums in Norway (TMB, ZMBN, ZMON, ZMTøN) have been examined. When relevant to our taxonomic goals, Recent and fossil material from Shetland and the Mediterranean was also studied.

The descriptions are primarily based on light microscopy (LM) and scanning electron microscopy (SEM). Standard procedures for SEM were followed (Geiger et al., 2007). To get a broader selection of material for description of variability, measurements were taken from LM photographs. Terminology follows Geiger (2003). Characters found to be of primary value in distinguishing species were: maximum size, shell shape, rate of increase in whorl width with growth, umbilicus width and presence or absence of a funiculus (a spiral cord in the wall of the umbilicus), the distance between selenizone and suture for the first few whorls, shape of aperture, especially inner edge and relation to umbilicus and any funiculus.

The sculpture is important and sometimes diagnostic, but generally rather variable. Details in the microsculpture of the protoconch and teleoconch I (e.g., Figure 1) are often important, but usually only visible in SEM images, and then only in fresh, uneroded shells.

Abbreviations used in the text are: DLG: Daniel L. Geiger collection, Los Angeles, USA; DMNH: Delaware Museum of Natural History, Wilmington, USA; JWC: John Wolff Collection, Lancaster, USA; MNHN: Muséum National d'Histoire Naturelle, Paris, France; MNW: National Museum Wales, Cardiff, United Kingdom; NHMUK: The Natural History Museum, London, United Kingdom; NHMW: Naturhistorisches Museum Wien, Vienna, Austria; NMR: Natural History Museum, Rotterdam, The Netherlands; NMSZ: National Museum Scotland, Edinburgh, United Kingdom; SBMNH: Santa Barbara Museum of Natural History, Santa Barbara, USA; SRC: Stefano Rufini Collection, Aguillara, Italy; TBS: Trondheim Biologiske Stasjon, Norway; USNM: National Museum of Natural History, Smithsonian Institution, Washington, USA; ZMBN: Zoological Museum, Bergen, Norway; ZMH: Zoologisches Museum, Hamburg, Germany; ZMON: Zoological Museum, Oslo, Norway; ZMTøN: Zoological Museum, Tromsø, Norway; ZMUC: Zoological Museum, Copenhagen, Denmark; H2DEEP: Ultraslow spreading and hydrogen based deep biosphere (Programme); MAREANO: Marine Areal database for Norwegian waters (Programme).

All material examined and not explicitely stated to belong to a particular museum collection has been deposited at the Zoological Museum in Bergen, Norway (ZMBN).

SYSTEMATICS

Anatomidae McLean, 1989

Anatoma Woodward, 1859

Type Species: *Scissurella crispata* Fleming, 1828 (by monotypy).

Remarks: *Anatoma* was long regarded as a subgenus of *Scissurella* d'Orbigny, 1824. *Schizotrochus* Monterosato, 1877 is an objective synonym. In the early 1960s *Anatoma* was rediscovered as the correct name for the group, but it was still regarded as a subgenus of *Scissurella*. Powell (1979) seems to have been the first to recognize that the conchological differences between *Scissurella* sensu stricto and *Anatoma* warranted full generic status for *Anatoma*. McLean (1989) introduced the taxon Anatominae at the subfamilial rank, to which Geiger and Thacker (2005) assigned full familial rank based on a molecular phylogenetic study. The family is found from Antarctica to the Arctic, from the intertidal to 5000 m, but is most common between 20 and 250 m (Geiger and Sasaki 2009). In inshore Norwegian waters, three species are found, and two additional ones in the Norwegian Sea.

Anatoma crispata (Fleming, 1828)

(Figures 1–18)

Scissurella crispata: Fleming, 1828: 385, pl. 6, Figure 3.

Scissurella crispata: Forbes and Hanley 1853: 544; Jeffreys 1865: 283; G.O. Sars, 1878 (in part): 126, pl. 8, fig. 7a, b; Norman, 1879 (in part?): 24; Schneider, 1886: 102; Norman, 1893 (in part?): 360; Friele and Grieg, 1901 (in part): 59; Brøgger, 1901 (in part?): 657, pl. 17, fig. 3; Norman, 1902: 357; Friele, 1903 (misidentification?): 15; Odhner, 1912 (in part): 13, pl. 2, figs 25–27; Dautzenberg and Fischer, 1912: 286; Soot-Ryen 1924: 50; Dautzenberg, 1927: 213; Odhner, 1960: 384; Fretter and Graham, 1976 (in part): 2; Bouchet and Warén, 1979 (misidentification?): 220; Graham, 1988: 60.

Anatoma crispata: Høisæter, 1986 (in part): 81; Sabelli et al., 1990 (misidentification?): 12; Smith and Heppell, 1991: 11.

Figure 1. *Anatoma crispata*, **neotype**. SEM. Shetland, Great Britain, 60°30′ N, 1°15′ W (NHMUK, 1849.10.5.5–7). Scale bar shell = 1 mm; Scale bar protoconch = 100 µm.

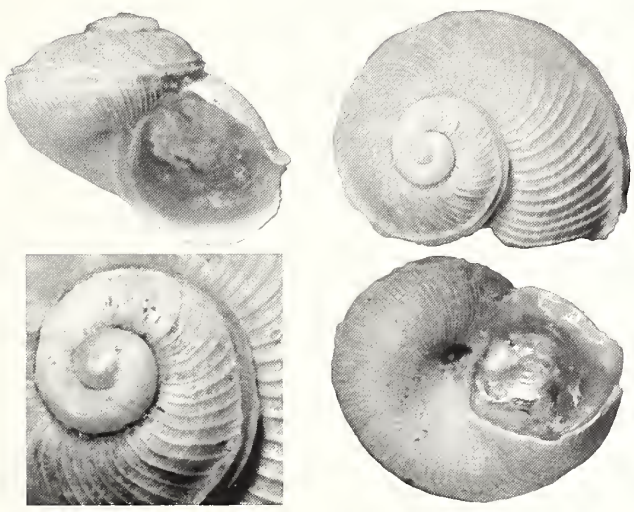


Figure 2. *Anatoma crispata*, Bremnesfjorden, Møre og Romsdal county, Norway (63°07′ N, 200–180 m), 2.1 mm diameter. Scale bar protoconch = 400 µm.

Scissurella angulata Lovén, 1846: 20 (see below under *A. tenuisculpta*).

Description: (Based mainly on the **neotype** [Figure 1] and a specimen from Bremnesfjorden, Norway [Figure 2]). Shell globular, small to moderate size (to 2.25 mm diameter, **neotype** 1.83 mm), trochiform, inflated, wider than tall. As in other species, juveniles "flatter" than adults. Protoconch of 0.75 whorls, with coarse flocculent sculpture, no apertural varix, apertural margin straight to slightly convex. Teleoconch I of 0.75 whorls, approximately 22 fine axials, weak spiral cord in position of selenizone. Teleoconch II of little less than two rapidly increasing, rounded whorls, suture adjacent to selenizone except near aperture of mature shells where up to five spirals separate suture and selenizone. Shoulder with 60–70 fairly strong axials on body whorl, sometimes rather crowded toward aperture; single spiral thread at or slightly behind start of selenizone, ca. 12–13 threads at apertural margin of mature shells, ⅓ to ½ width of axials. No spirals in adsutural 15% of shoulder. On base, 16–20 spirals cross the up to 65 rather strong axials, creating a grid-like pattern, approximately one of six to ten axials disappear at mid-base, remaining axials spirals into not very wide umbilicus. Rather narrow funiculus joins lower lip at columella starting point. Selenizone at periphery, of varying width but mostly wide, keels distinct, growth marks at least partly coordinated with axials. Margins of slit parallel. Aperture rounded, roof overhanging.

Operculum (Figure 2): Round, covering aperture, thin, transparent, multispiral, with central nucleus.

Radula (Figures 3–7): Rachidian tooth trapezoid, central cusp isolated, on either side four cusps arranged in fan shape. Lateral teeth 1–3, similar, innermost of 3–4 cusps largest. Lateral tooth 4 reduced, outermost of four cusps largest. Lateral tooth 5 enlarged, four cusps on inner margin, terminal one largest, one cusp on outer margin. Inner marginal teeth with triangular tip, terminal cusp largest, inner margin with four small cusps, outer margin with five larger cusps. Outer marginal teeth spoon shaped, approximately eight fine cusps on either side.

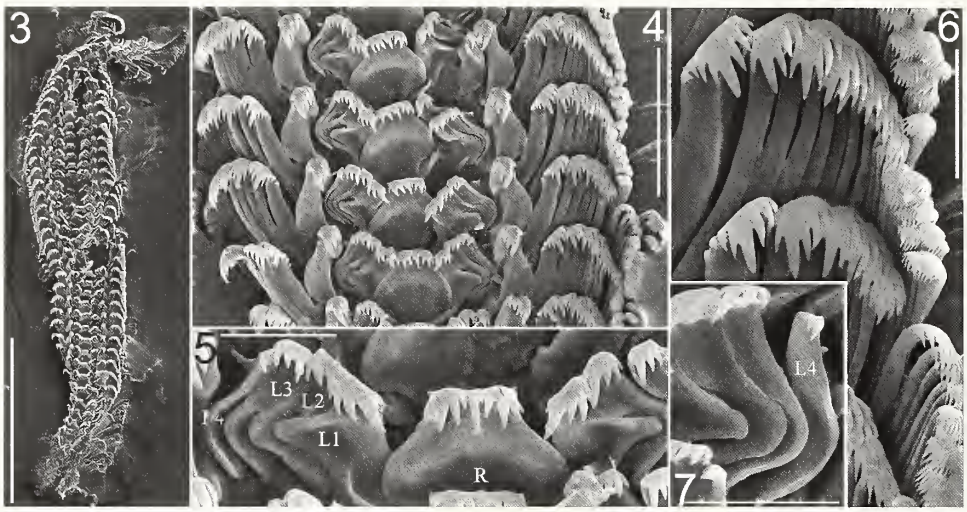
Differential Diagnosis: *Anatoma tenuisculpta* reaches a much larger size than *A. crispata* (5 mm vs. 2.25 mm) and is less globular and with more regular sculpture; it has no funiculus at any growth stage. The protoconch is smaller (216 vs. 255 µm) and the whorls increase more slowly. The shoulder is less convex, as is also the base. The edges of the slit and selenizone are also more regular than in *A. crispata*, and the slit has slightly converging margins in mature shells.

Anatoma aspera is taller and has a smaller protoconch (172 vs. 255 µm) and "tighter" spiral whorls, with a wide-angled funiculus starting fairly deep inside the umbilicus. The suture is significantly below the selenizone. The selenizone keels are wider, more prominent, and the axials on the shoulder are stronger, more "costae"-like.

Anatoma schioettei is more lenticular, has a distinct space between the start of the selenizone and the suture of the subsequent whorl, and has about half as many and more distinct axials.

Anatoma schanderi has a much larger shell (4.5 vs. 2.25 mm), is more turreted, has reticulate protoconch sculpture, and the axials are weaker and more similar in strength to the spirals.

Type Material: Whereabouts of Fleming's syntypes are unknown (McLean, 1967); they could not be found in either NHMUK, NMW, or NMSZ, and are presumed



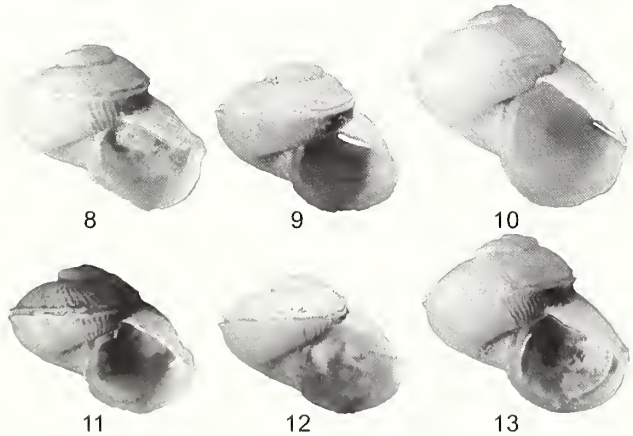
Figures 3–7. *Anatoma crispata*, radula, Fleslandsskjær, Raunefjorden, Hordaland, Norway, 60°18′ N, 5°13′ E, (DMNH 23176, 1). **3.** Whole radula. Scale bar = 200 µm. **4.** Whole width of radula. Scale bar = 30 µm. **5.** Central field with raehidian tooth (R) and lateral teeth 1–4 (L1–4). Scale bar = 10 µm. **6.** Marginal teeth. Scale bar = 10 µm. **7.** Lateral tooth 4. Scale bar = 10 µm.

to be lost. **Neotype** here designated, Shetland, Great Britain, 60°30′ N, 1°15′ W, NHMUK 1849.10.5.5-7.

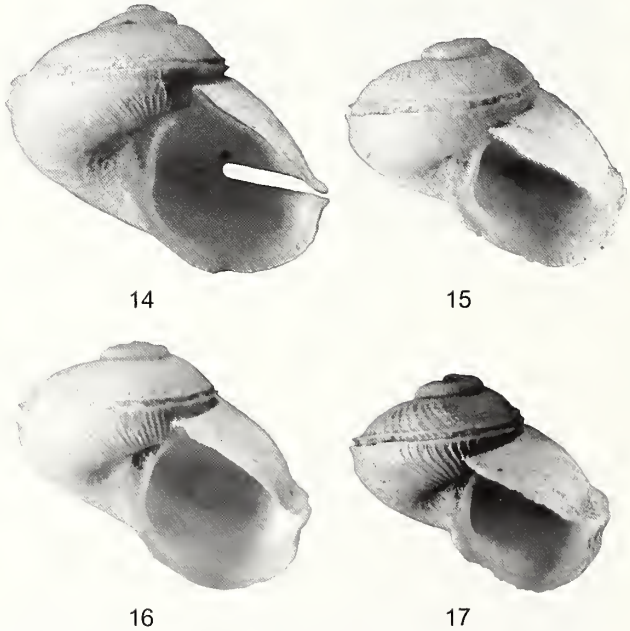
Type Locality: Noss Island [outside Lerwick] in Shetland (60°10′ N, 1°00′ W), where it was found in shell sand on the beach after a storm (Jeffreys, 1865).

Other Material Examined: 20/7 specimens/shells from Skagerrak, 29/15 from western Norway (own material), 0/10 (ZMON), 1/1 (ZMBN); 65/307 from middle Norway (63–65° N) (own material); 152/135 from northern Norway (66–71° N) (own material), 9/41 (ZMON), 4/0 (ZMBN), 4/20 (ZMTø). Material from Shetland 0/37 (NHMUK, MNHN, NMSZ).

Variability: *Anatoma crispata* has a wide distribution, both geographical and bathymetrical, and its shell morphology varies accordingly. Thus it is possible to recognize certain geographical morphotypes along the Norwegian coast (Figures 8–13, 15 and 17), as specimens from northern Norway (67–68° N) are somewhat larger (to 2.23 vs. 2.03 mm) and much more globular than those from further south (H/D varies from more than 0.9 to 0.8 or less). The shell morphology of the **neotype** (from Shetland, Figure 1) falls within the variation seen among



Figures 8–13. *Anatoma crispata*, six specimens from inshore Norwegian waters. **8, 11.** South coast (58°15′ N, 90–80 and 57 m respectively). **9, 12.** West coast (60°30′ N, 70–75 and 190 m respectively). **10, 13.** North coast (67°10′ N, 30 m). All specimens to scale, the largest (10) 2.23 mm diameter.



Figures 14–17. *Anatoma crispata*, four specimens from ea. 62–63° N. **14, 16.** Iceland-Faroe Ridge (63°35′ N, 12°51′ W, 574 m). **15, 17.** Coast of Møre og Romsdal (62°28′ N, 120–60 m). All specimens to scale, the largest (14) 2.42 mm diameter.

Figure 18. *Anatoma angulata*, **lectotype, here designated,** SEM (SMNH 4394), 2.25 mm diameter. Scale bar shell = 1 mm; Scale bar, protoconch = 100 µm.

inshore southern Norwegian specimens (Figures 2 and 8–13).

Shells from the southern side of the Iceland-Faroe ridge (Figures 14 and 16) are larger (to at least 2.45 mm) than material from inshore Norwegian waters at roughly the same latitude (Figures 15 and 17) which do not surpass 2.25 mm.

Distribution: Based on literature data the species is widely distributed, from the Mediterranean to the Barents Sea, from several hundred meters in fjords and the upper slope, to 10–20 m in northern Norway. It is, however highly doubtful that *Anatoma crispata* really occurs in the Mediterranean, as all Mediterranean specimens previously identified as *A. crispata* belong to different species (*A. aspera*, *A. tenuisculpta*, *A. eximia* (Seguenza, 1877), *A. umbilicata* (Jeffreys, 1883), *A.* new species Geiger, ms), and all illustrations of sufficient quality show species other than the true *A. crispata*). The main distribution is probably the northern part of the North Atlantic, in special the coast of Norway. The distribution extends south along the western coast of Britain and Ireland and farther south, but is insufficiently documented south of Ireland.

In material examined, there are specimens from 12–15 m (Vefsnfjorden, 65° 52′ N) and 20–10 m (Trondheimsleia, 63°24′ N) to 848 m (upper slope at 68° 39′ N, Mareano) and an empty shell from 1083 m (on the slope at 69° N, Mareano). Inshore, it is found down to 200–180 m in Bremnesfjorden, (Figure 2) and 190 m (Hjeltefjorden, 60°33′ N) and empty shells at 680 m in Korsfjorden (60°08′ N). The majority of living specimens have been taken between 70–50 m in southern and western Norway, and 40–25 m in northern Norway.

Remarks: *Anatoma crispata* is the first described species of the family, and has consistently been confused with a host of other species worldwide (e.g., the Australian *A. australis* (Hedley, 1903) and the northeastern Pacific *Thieleella kelseyi* (Dall, 1905): see Geiger and Jansen 2004a, Geiger and McLean, 2010, and also *A. atlantica* Bandel, 1998: see Tunnell et al. 2010) and in north-European waters with at least two other species treated here. Beginning with Jeffreys (1877), a number of species have been described from various deep water expeditions in the North Atlantic, but, until recently, few attempts have been made to subdivide the ubiquitous "*A. crispata*" on the shelf/upper slope of mainland Europe. The first may have been Dautzenberg (1927) who decided that the available evidence favored *A. aspera* to be a distinct species rather than just a variety of *A. crispata*. Nevertheless, until around 2000, most checklists still listed *A. crispata* as the only member of the European marine fauna, sometimes in addition to the deep water species *A. umbilicata* (Jeffreys, 1883) another mostly misidentified species (see entry for this species below).

In summary, the identity of *A. crispata* is highly confused, both regionally as well as globally. Additionally, *A. crispata* is the type species of the genus *Anatoma*, but the whereabouts of Fleming's syntypes is unknown. Accordingly, we designate here a **neotype** with the explicit intent to stabilize the nomenclature of the taxon. The specimen selected is from as close to the original type locality as possible (Shetland Islands) and corresponds to Fleming's (1828) description and illustration as well as possible. It is a well-preserved specimen with the protoconch. The specimen is at 1.83 mm slightly larger than Fleming's measurement of 1/15″ [=1.67 mm].

Given the equally contentious identity of *A. angulata* (see also under *A. tenuisculpta* below), we designate herein the sole surviving syntype (SMNH 4394) of the species as the **lectotype** (Figure 18), with the explicit purpose of nomenclatural stabilization of this taxon, in case non-conspecific syntypes should be located.

The present work documents that both *A. aspera* and *A. tenuisculpta* are distinct from *A. crispata*, and that these three species are all members of the Norwegian fauna. Even *A. crispata* sensu stricto seems to be a variable taxon, with a very wide distribution, both geographically and bathymetrically. In Norwegian waters, it dominates the samples from northern Norway (north of 64°N). Most (but not all) of the live-caught specimens from this part of the coast are from shallow (10–25 m), inshore, hard-bottom, environments. Museum-material documents it from the eastern, cold-water Barents Sea (71°42′ N, 271 m, –1.4°C) (ZMBN 21014), and Bøkfjord in Sør-Varanger (15–10 m) (ZMTø St. 4, 24/6 1937), as well as from Vadsø in Varangerfjorden (ZMON D 391). Southward, it is found around the Skagerrak coast, at least east to 9° E, near Risør. Hansson (2003) and Warén (pers. comm.) report that, in the last few decades, this species has become very scarce on the west coast of Sweden, after having been regularly collected in

earlier years. It is unclear whether this is the case also for the south coast of Norway. A number of the specimens from the Skagerrak coast were collected by Per Wikander in 1986–1988 (see further below under Remarks for *A. aspera*).

***Anatoma aspera* (Philippi, 1844)**
(Figures 19–33)

Scissurella aspera Philippi, 1844: 160, pl. 25, Figure 17.
Scissurella aspera: Weinkauff, 1862: 349; Munier-Chalmas, 1862: 396; Hidalgo, 1867: 144; Norman 1888: 21; Odhner, 1960: 385, 387.
Scissurella crispata var. *aspera*: Jeffreys, 1883: 88; Odhner, 1912: 13, pl. 2 fig. 25.
Schizotrochus asper: Monterosato, 1884: 39; 1890: 143.
Scissurella (Schizotrochus) aspera: Dautzenberg, 1927: 213.
Anatoma aspera: Anistratenko and Starobogatov, 1997: 76, fig. 4; Ardovini and Cossignani, 2004: 19; (misidentified: is *A. tenuisculpta* their *A. crispata* is *A. aspera*); Høisæter, 2009: 20.
Anatoma crispata Giannuzzi-Savelli et al., 1994: 13 (is *A. aspera*).
Scissurella crispata var. *paucicostata* Jeffreys, 1865: 284 [Figure 27 below].

Description: (Based mainly on **neotype** (Figure 19) and specimen from Raunefjorden, Hordaland county, (Figure 20)). Shell globular, of medium size (to 3.3 mm diameter). Height equal to or slightly less than diameter. As in other species, juveniles "flatter" than adults. Protoconch (Figures 21–22) of 0.75 whorl, with wide, open, irregular sculpture; varix present (in some specimens apparently doubled), barely connected to embryonic cap. Teleoconch I of 0.75–1 whorl, 20 (or more) axials, often partly eroded in larger shells, interaxials smooth except for strong spiral cord in position of selenizone (may also be eroded in larger shells). Teleoconch II up to 3¼ rapidly increasing whorls, with 5–12 spirals on base, visible between suture and selenizone. Shoulder with up to 65–67 high, crest-like axial costae on body whorl, additional fine axials on keel of selenizone; at least 15 very fine spirals in interaxials, an order of magnitude finer than axials, and not crossing the latter. On base, 25–30 spirals cross up to 90 slightly sinusoid axials creating a grid-like pattern (axials dominating but finer and denser than axials on shoulder); some axials disappear at midbase; remaining axials spiral into wide, deep umbilicus. Characteristic, almost triangular, funiculus departing columellar lip at roughly 40–45° near upper end of latter. Selenizone at periphery or a little above, wide (15–20% whorl height), keels distinct, somewhat flaring, growth marks not coordinated with axials. Margins of slit parallel. Aperture round, columellar lip somewhat flared, partly obscuring the umbilicus. Shell grayish white, empty shells often glassy, transparent, often with blackish "deposit" in some of cavities created by grid-like sculpture on base. "Dirty" aspect of specimen in Figure 20 largely representative of Norwegian specimens.

Operculum: Round, covering aperture, thin, transparent, multispiral, with central nucleus.

Radula (Figures 23–26): Rachidian tooth with central cusp strongest, curved arrangement of 3–4 cusps on each side. Lateral teeth 1–3 similar, apical cusp strongest, 3–4 on outer edge. Lateral tooth 4 smaller, apical

Figure 19. *Anatoma aspera*, **neotype**, Terreti - Cellantoni Bridge, 567 m above sea level, Pleistocene epibathyal facies, muddy clay, Italy, 38°07′ N, 15°43′ E, SBMNH 149681, 2.66 mm diameter.

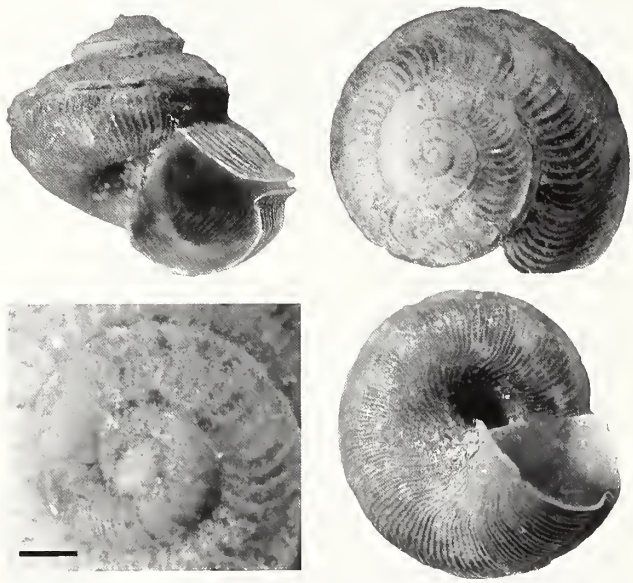
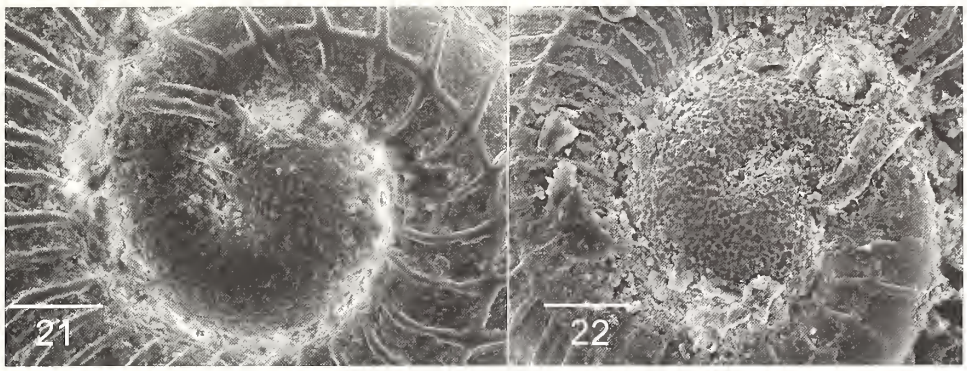
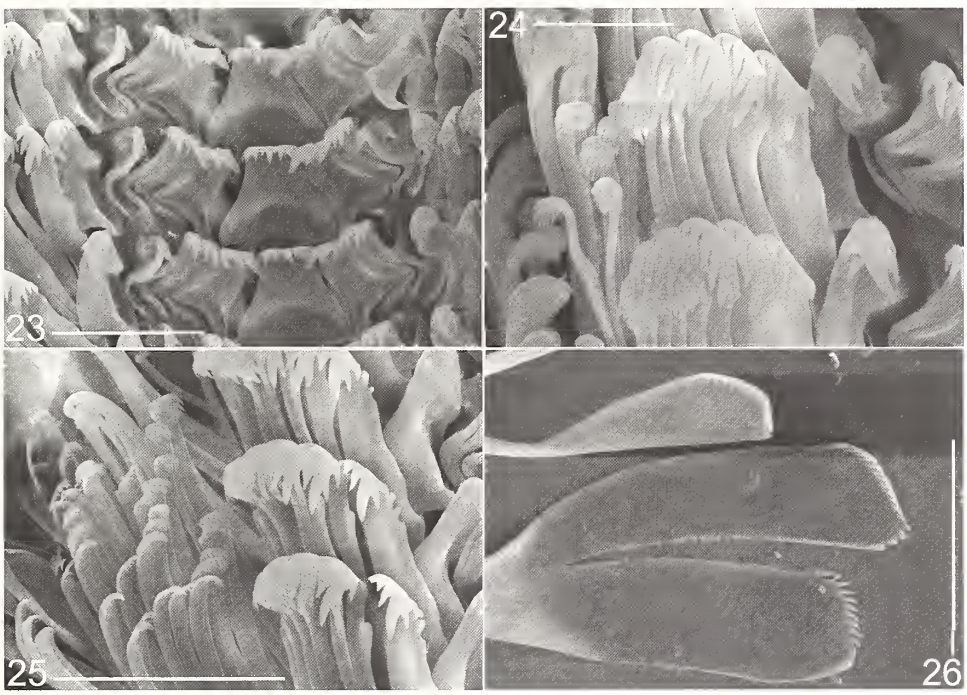


Figure 20. *Anatoma aspera*, Liholmsrennen, Raunefjorden, Hordaland county, (60°18′ N, 70–55 m), 5 mm diameter. Scale bar protoconch = 100 µm.



Figures 21–22. *Anatoma aspera*, protoconchs. **21.** Northern Tyrrhenian Sea, Italy. 70–100 m (DLG 311, 6). **22.** Liholmsrennen, Raunefjorden, Hordaland, Norway, 60°18′ N, 5°09′ E, 70–55 m. Scale bars = 50 µm.



Figures 23–26. *Anatoma aspera*, radula, Liholmsrennen, Raunefjorden, Hordaland, Norway, 60°18′ N, 5°09′ E, 70–55 m. **23.** Central field. **24, 25.** Marginal teeth. **26.** Outermost marginal teeth. Scale bars 23, 25 = 20 µm; 24, 26 = 10 µm.

cusp strongest, 3 smaller cusps on inner margin. Lateral tooth 5 elongated, apical cusp largest, approximately 6 cusps on inner edge. Inner marginal teeth inequilaterally triangular, apical cusp largest, 3 on inner margin, 4–5 on outer edge, outer marginal teeth with spoon-shaped tip. Outermost marginal teeth paddle-shaped with many small bristles at distal edge; no food groove. Radular interlock of central field moderate.

Differential Diagnosis: *Anatoma tenuisculpta* is larger than *A. aspera* (5 vs. 3.3 mm) and wider at same height, and has much narrower space between the suture and the selenizone at any given number of whorls; the former has a much finer axial sculpture, and more regular and prominent spiral sculpture. The distance between axials is more or less the same above and below the selenizone in *A. tenuisculpta* and with less dominating axials on the shoulders. In *A. tenuisculpta*, the keels of the slit and selenizone are less prominent, and the width of the selenizone is about 20% smaller. There is no funiculus in the narrower umbilicus. The shell is often yellowish gray-white although this varies in preserved material. The axial sculpture on the base is evenly rounded, and the base is sloping more gradually down from the selenizone.

Anatoma crispata is smaller (2.25 vs. 3.3 mm), more globular, and somewhat wider at same height; the axial sculpture on the shoulder is less dominating and the axial sculpture on shoulder and base is equally well developed. On early whorls, the suture is immediately below

the selenizone, whereas in large specimens it is less than half the selenizone width. The keels of the selenizone are not as prominent and the selenizone is narrower. The protoconch is larger and the whorls increase more rapidly in width. The umbilicus is narrower and with a distinct funiculus starting at lower end of umbilical lip.

Figure 27. Holotype of *Anatoma crispata* "var. *paucicostata*," USNM 181580. Scale bar shell = 1 mm; Scale bar protoconch = 100 µm.

Anatoma schioettei has a much smaller (2.15 vs. 3.3 mm) shell, is much more disc-shaped, and has fewer axials that are crossed by almost imperceptible spirals.

Anatoma schanderi is larger (4.5 vs. 3.3 mm) has weaker axial sculpture that is approximately as strong as the spirals, sculpture on shoulder and base are approximately equally developed, and the protoconch has reticulate sculpture.

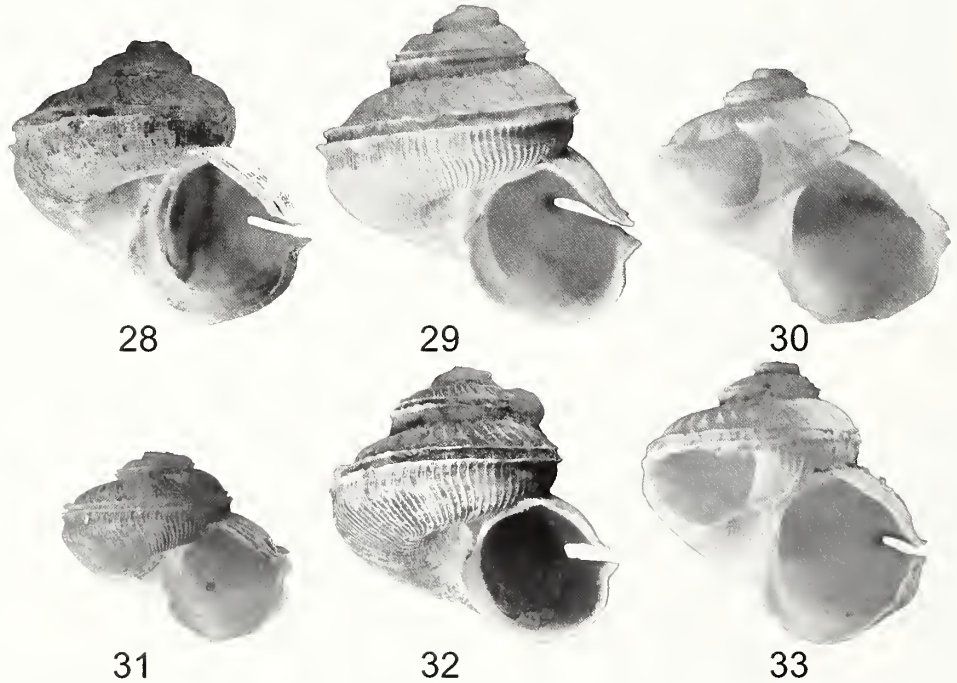
The radula of *A. aspera* is similar to the one of *A. tenuisculpta* and *A. schanderi*, in that the rachidian has a dominating central cusp with three smaller ones on each side, and wide lateral teeth 1–4 each with seven long and narrow cusps, the innermost dominating.

Type Material: Whereabouts unknown (not in Hamburg), presumed to be lost. **Neotype** is here designated, Terreti-Cellantoni Bridge, Italy, 38°07′ N, 15°43′ E, 567 m above sea level, Pleistocene, epibathyal facies, muddy clay, SBMNH 149681.

Type Locality: Punta Pezzo 13 km north of Reggio, Calabria, across the Strait of Messina from Sicily. Fossil of Pleistocene age from shelf deposits.

Other Material Examined: 42/52 specimens /shells of own material, 1/13 from the collections of ZMON, 6/9 from ZMBN, 1 shell from Trondheim Biologiske Stasjon, 0/1785 from throughout its range in various collections.

Variability: Figures 28–33 illustrate some of the variability of the species along the coast of Norway. The



Figures 28–33. *Anatoma aspera*, six specimens from the coast of Norway. **28, 31.** Raunefjorden, Hordaland county (60°18′ N, 70–55 m and 60°17′ N, 70–80 m). **29, 32.** North of Kirkelandet, Møre og Romsdal county (63°10′ N, 145 m). **30, 33.** Mouth of Andfjorden, Steinvær-revet, Nordland county (69°13′ N, 370 m). All specimens to scale, the largest (29) 3.3 mm diameter.

neotype (Figure 19) and the holotype of *A. crispata* "var. *paucicostata*" (Figure 27) from Shetland further testify to the morphological diversity of this species. The main variability seems to be associated with whorl expansion rates. Thus H/D ratios vary between 0.90 and 1.08 in Norwegian specimens of roughly the same size. The relative steepness of the shoulder (Figure 29 vs. 30) contributes to the different appearances of the shells as well. Further the relative strength of spirals and axials on the base varies (compare Figures 28 and 32). Three empty shells found around 69° N (Figures 30 and 33) have an extreme shape with the body whorl dominating completely, a wide selenizone and a longer more "*crispata*" like funiculus than in the forms found further south along the coast. Norwegian specimens generally reach a larger size than their Mediterranean counterparts, with maximum measured diameter of Mediterranean shells at 2.4 mm. The selenizone is generally wider and more open in Mediterranean specimens (see Figures 19 and 20).

Distribution: According to the literature and available museum material, mainly Mediterrancan but also from the lower shelf and upper slope north along the Portuguese, Spanish and French coasts, and off the Irish and British western coasts. There are several lots from Rockall Trough between 550 to 680 m, a single lot from Porcupine Bank at 773 m, and a single specimen from the lower shelf north of the Faroes (250–400 m). Based on examined material, the species is found in Norway from Mosterhavn in Hardangerfjorden (59°42′ N) to Andfjorden (69°15′ N), but with a significant gap in distribution between 64°–69° N. (Possibly some of the 37 records of *Anatoma crispata* in Sneli et al. (2005) reporting the results from BIOFAR could represent *A. aspera*).

Remarks: The fossil assemblage described by Philippi (1844) is most likely a mixture of species of Pliocene to late Pleistocene age. This may be inferred from the frequent and sharp changes in depositional characters and fossil content due to strong Plio-Pleistocene tectonics at the location (Barrier, 1987). Thus, it is not unreasonable to accept Philippi's name for the Recent species discussed here. One of the leading fossils in the assemblage is in fact *Modiolula phascolina* (Philippi, 1844), which is regarded in Norway as a "carpeting" species, creating a preferred substrate for a number of species at intermediate depths (50–200 m) in the fjords. The three inshore species of *Anatoma* discussed here are often found together with this bivalve. *Anatoma aspera* has been recognized as a valid Recent species in the Mediterranean by most conchologists. Weinkauff (1862) reported it from "Alger; très-rare"; Munier-Chalmas (1862) reported it also from Alger (may be the same record) and, surprisingly, from "Berghen, (Norwège)"; Hidalgo (1867) found a single, empty, but well preserved shell in the stomach of the fish *Peristedion cataphractum* (Linnaeus, 1758) near Mahon in Menorca (Balearic Islands, Spain). Later, Monterosato (1884) claimed that it was known from many localities in the Mediterranean, in contrast to *A. crispata*, which he claimed was scarce in the Mediterranean and the Adriatic Sea. Monterosato (1890) reported it without further comments as a member of the deep muddy bottom fauna near Palermo. (See also remarks above on possible confusion of *A. tenuisculpta* with *A. crispata*).

During the 1860s and 1870s, the species was not reported from the Atlantic, and Jeffreys (1865: 285) clearly had not seen it when he wrote: "Believing the *S. aspera* of Philippi to be the same species as *S.angulata* of Lovén, and that the latter is merely a large form of *S. crispata*,...". He thus set a pattern for *A. aspera* to be considered a variety of *A. crispata*. That Jeffreys was not familiar with Philippi's species is evident from his naming of a new variety of *A. crispata* "var. *paucicostata*" in the same work: "Spire more raised, and the ribs on the upper side much fewer than usual" (Figure 27, holotype). This variety was based on material from Shetland. Jeffreys (1877: 234) stated "I regard *S. aspera* of Philippi as a variety of the present species [i.e. *S. crispata*]. The height of the spire is an unreliable character". Later (Jeffreys 1883:88), he synonymized the two varieties, "*S. angulata* of Lovén and *S. aspera* of Philippi are varieties [of *A. crispata*]; the latter corresponds with my variety *paucicostata*."

During the 1890s, *A. aspera* was reported from fairly deep water (1200–1400 m) in several localities in the southern North Atlantic (e.g., Jeffreys, 1883; Locard, 1899). Some considered it to be a distinct species, others as a variety of *A. crispata*. Dautzenberg (1927), although recognizing a number of gradually converging conchological characters, regarded it as a valid species with a more southern distribution than *A. crispata*. Dautzenberg (1927: 214) arguments for accepting it as a valid species (reversing his opinion in Dautzenberg and Fischer 1912): "...car l'*aspera* est constamment plus petit, sa spire est beaucoup plus élevée, ses tours sont étagés et ses plis longitudinaux plus accusés." ["because *aspera* is consistently smaller, its spire is much more elevated, its whorls are stepped and its longitudinal folds are more prominent"].

Most non-Mediterranean authors (G.O. Sars, 1878; Norman, 1879; Dautzenberg and Fischer, 1912 chose to follow Jeffreys rather than Monterosato and later Dautzenberg; Odhner (1912), and most later authors either mention *A. aspera* as a variety of *A. crispata*, or report *A. crispata* as the only species found in northeast Atlantic waters (e.g., Fretter and Graham, 1976, Smith and Heppell, 1991). This tradition has also been adopted by most recent Mediterranean authors (Sabelli et al., 1991, citing Schirò, 1986). Clear evidence of the confusion is found in Giannuzzi-Savelli et al. (1994), in which illustrations of *A. aspera* are misidentified as *A. crispata*.

In discussing the *Anatoma* spp. collected by the Swedish Josephine Expedition in 1869, Odhner (1960)

mentioned *A. aspera* (as a full species) from Josephine's Bank (ca. 380 km due west of the southern tip of Portugal, 200–935 m depth), in addition to three West Indian localities ranging from 180–720 m depth. These records from moderately deep water are supplemented by three records by Dautzenberg (1927) from around the Azores and the Canaries at 1230–1350 m. We have not been able to locate any references to *A. aspera* as a full species from northern waters in more recent literature.

Anatoma aspera thus seems to be known as a Recent species from three or four different geographic/bathymetric zones, the Mediterranean in moderately deep water (20–1200 m: collection records DLG, MNHN) in the southern part of the North Atlantic on or near seamounts, from 200 m to 4400 m (collection records RMNH from Azores), and in Norwegian inshore waters [plus the record of *S.* "var. *paucicostata*" from Shetland by Jeffreys (1865)]. A statement that indicates that the material from the southern part of the North Atlantic might be specifically different from our northern form, is that according to Dautzenberg (1927: 214 [translated from French]) "*aspera* is consistently smaller [than *A. crispata*]", which does not fit the Norwegian material. The Norwegian shells of *A. crispata* never reaches the size (maximum diameter 2.4 mm) of a fully grown *A. aspera* (maximum diameter at least 3.3 mm). Mediterranean specimens, however, seem generally to be smaller than Norwegian specimens (to 2.5 mm).

In Norwegian waters, the species is definitely less common than *A. crispata*, and is mainly a southern form. Except for three shells from a *Lophelia* reef at 69°14′ N, we have no records of specimens from north of 64°40′ N. Two shells from the collection of the Zoological Museum in Tromsø, from respectively Lofoten and Bjarkøy (ca. 69° N) may also belong to this species. The species is rarely found shallower than 50 m or deeper than 150 m, and the blackish "deposit" on all or part of the shell (Figure 20) indicates that its microhabitat is somehow associated with blackish, maybe anoxic, sediment.

It is perhaps of importance that in three recent (Sep.–Oct. 2007) attempts to obtain some new material from one of the most reliable localities from the 1960s, only specimens of *A. aspera* have been found, and only two specimens at that, whereas more than 30 specimens of all three species were collected in a single sample in the 1960s.

Given the confusing identities of the specific epithets *crispata* and *aspera*, representing species for which no type material is extant, it is important to stabilize both taxa by designating neotypes. We designate here a **neotype** for *A. aspera*, with the explicit intention of taxon stabilization. As discussed above, the species was described based on Pleistocene fossil material and is widely recognized as extending its temporal range into the Recent. We have selected a fairly well-preserved fossil specimen from as close as possible to the original type locality.

Anatoma tenuisculpta (Seguenza, 1877)

(Figures 34–47)

Scissurella tenuisculpta Seguenza, 1877: 273, pl. 16, Figure 29.
Scissurella tenuisculpta: Monterosato 1890: 143; Vazzana, 1996: 150, Figure 13.
Anatoma tenuisculpta: Lozouet 1986: 114.
Scissurella crispata auct. not Fleming, 1828: Lovén, 1846: 20; Jeffreys 1870: 444; Friele 1874: 15; G.O. Sars 1878 (in part): 126; Norman 1879 (in part?): 24; 1893(in part?): 360; Friele and Grieg (in part): 59; Brøgger(in part?) 1901: 657; Odhner 1912 (in part): 13; Grieg 1914: 76; Hubendiek and Warén 1974: 25; Fretter and Graham 1976 (in part): 2.
Scissurella crispata var. *angulata* auct. not Lovén, 1846: Odhner 1960: 384.
Scissurella argutecostata Seguenza, 1877: 273, pl. 16, Figure 30.
Scissurella funnazzensis de Gregorio, 1889: 13, pl. 1, fig. 9a–d.
Anatoma umbilicata auct. not Jeffreys, 1883.
Anatoma n.sp. Høisæter 2009: 21.

Description: (Largely based on **neotype**, Figure 34, and specimen from Tomfjorden, Norway, Figure 35 and from Rovdefjorden, Norway, Figure 36). Shell large (to 5.0 mm diameter), trochoid, biconical, wider than high, particularly in juveniles. Protoconch of slightly more than 0.75 whorls, with very fine flocculation; apertural varix not connected to embryonic cap, apertural margin slightly sinusoid. Teleoconch I of 0.5 to 0.65 whorls, with 17–30 fine axial cords, often partly eroded, spiral cord in position of selenizone. Teleoconch

Figure 34. *Anatoma tenuisculpta*, **neotype,** SEM, Terreti-Cellantoni Bridge, 567 m above sea level Pleistocene epibathyal facies, muddy clay, Italy (38°07′ N, 15°43′ E), SBMNH 149680, 3.55 mm diameter.

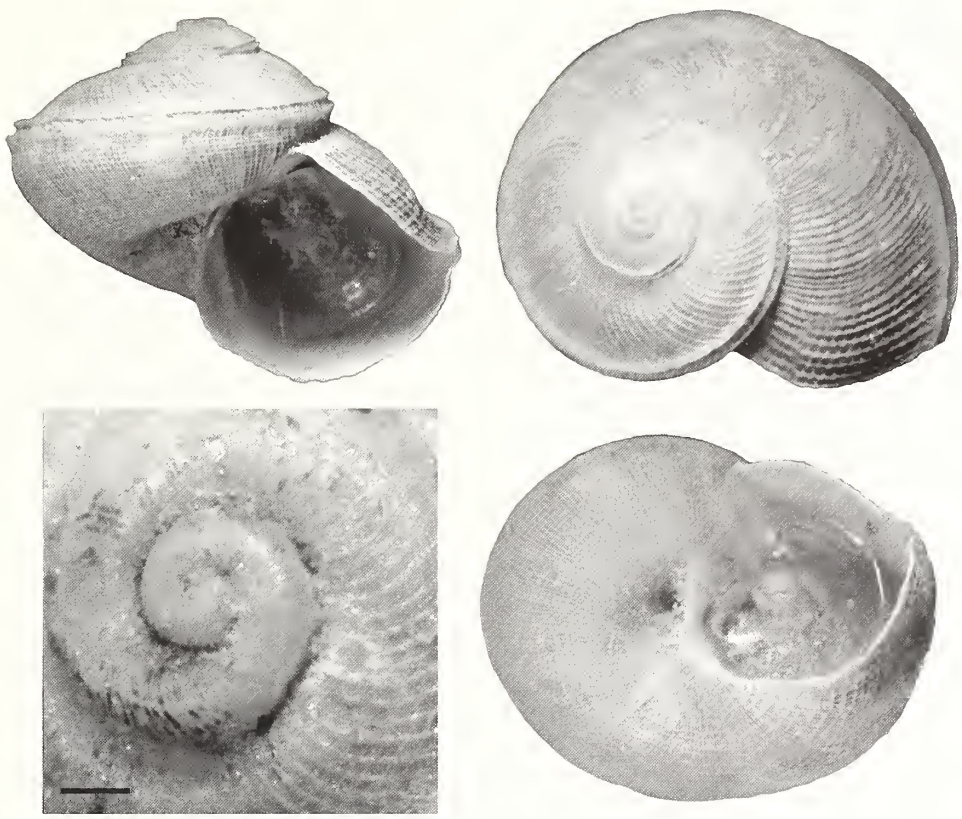


Figure 35. *Anatoma tenuisculpta*, Tomfjorden, Nordland county, Norway (66°15′ N, 380–300 m), 4.1 mm diameter. Scale bar protoconch = 100 µm.

H up to three whorls, suture approximately one to three selenizone widths below selenizone (one to three spirals between suture and selenizone), convex shoulder with 89–90 axials on body whorl (5 mm specimen); spirals starting with one median spiral between axials 4 and 5, after two axials, one new spiral on each side of first (all three on slightly concave lower part of shoulder), number of spirals increasing rapidly to 8–10 on next half whorl, then gradually to 17–18 spirals at aperture; spirals one order of magnitude finer than axials, not crossing axials completely, but creating a series of small nodules on axials of body whorl. Adsutural spiral-free band not much wider than distance between spirals. Base slightly convex, with 28–30 spirals crossing approximately 130 (5 mm specimen) only slightly stronger axials, creating regular grid of rectangular "pits"; these axials descending into fairly wide, deep umbilicus. Umbilicus open, without funiculus. Selenizone at periphery, narrow, keels distinct, axial lamellae distinct at least partly coordinated with axials. Margins of slit mostly parallel but slightly converging towards end. Aperture round; lower, inner lip flared, especially in juveniles. Columellar lip evenly rounded. Snails collected alive with translucent, yellowish hue, with rust-colored deposits in pits of sculptured surface.

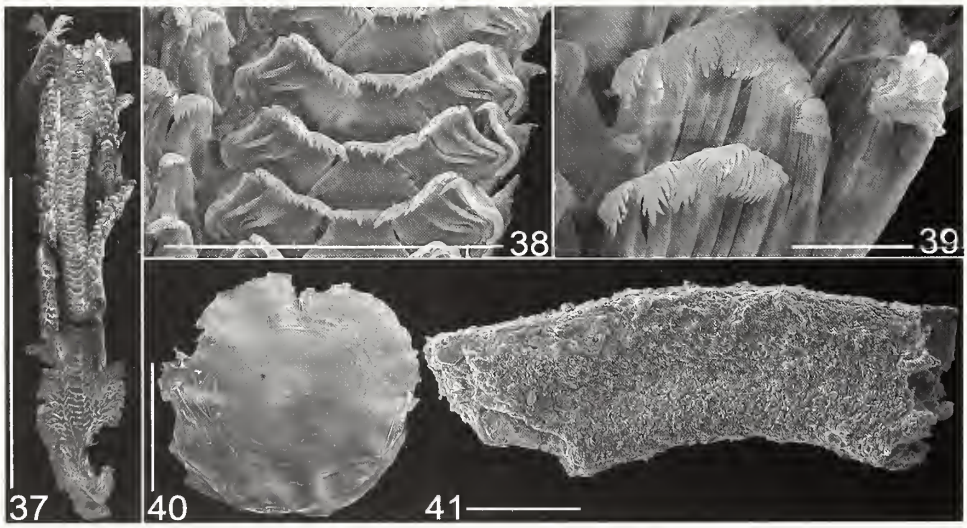
Operculum (Figure 40): Round, thin and transparent, multispiral with central nucleus.

Radula (Figures 37–39): Rachidian tooth trapezoid, apical cusp largest, five cusps on each side. Lateral teeth 1–3 similar, innermost lateral tooth with five cusps, innermost largest. Lateral teeth 2 and 3 similar with each four equal-sized cusps. Lateral tooth 4 reduced, narrow with a single cusp. Inner marginal teeth with triangular tip, apical cusp largest, 5–6 cusps on each side. Outer marginal teeth with spoon shaped tip, many fine bristles. Radular interlock of central field moderate.

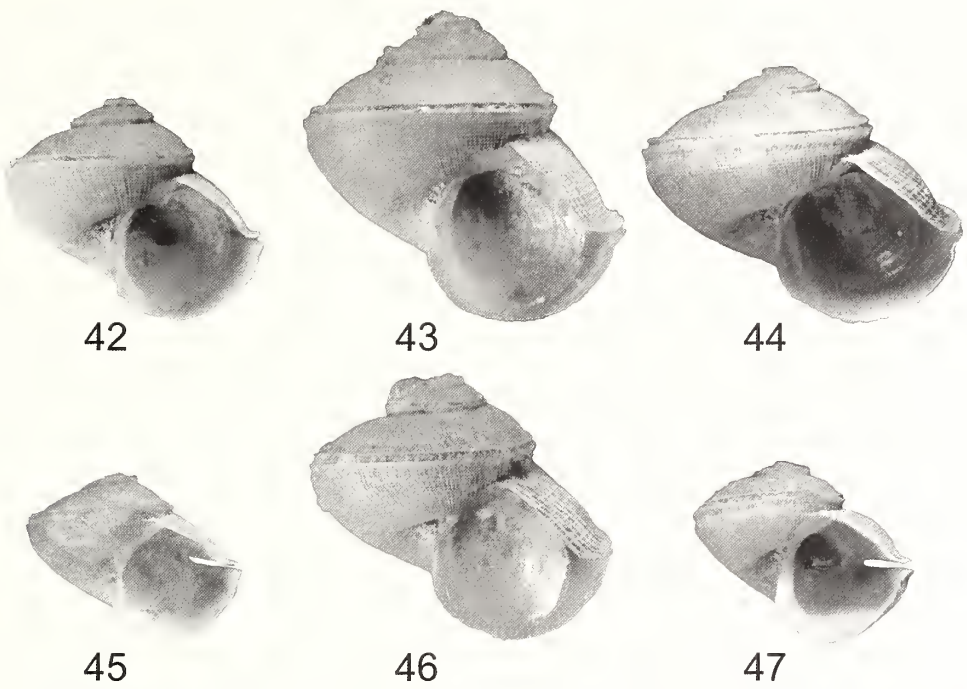
Gut content (Figure 41): Amorphous matter.

Differential Diagnosis: *Anatoma aspera* is proportionally taller and smaller than *A. tenuisculpta* (3.3 vs. 5 mm), with much coarser and less regular axial sculpture, and less prominent spiral sculpture on the shoulder. There is a pronounced gap between the suture and the selenizone above, particularly in larger specimens. The selenizone is wider and the margins of the slit are not converging. It has a wide-angled funiculus deep inside the wide umbilicus. The curvature of both shoulder and base is more convex, meeting the lower selenizone keel at nearly a right angle.

Figure 36. *Anatoma tenuisculpta*, SEM. Specimen from Rovdefjorden, Møre og Romsdal county, Norway (62°12′ N, 200–150 m), 3.8 mm diameter. Scale bars shell = 1 mm; Scale bar protoconch = 100 µm.



Figures 37–41. *Anatoma tenuisculpta*, 3.8 mm diameter. SEM. Radula, operculum and fecal pellet. A specimen from Rovdefjorden, Møre og Romsdal county, Norway (62°12′ N, 200–150 m). **37.** Entire radula. Scale bar = 200 µm. **38.** Central field. Scale bar = 20 µm. **39.** Marginal teeth. Scale bar = 10 µm. **40.** Operculum. Scale bar = 1 mm. **41.** Gut content of amorphous matter. Scale bar = 100 µm.



Figures 42–47. *Anatoma tenuisculpta,* six specimens from the coast of Norway. **42.** Straumsberget, Korsfjorden (60°10′ N, 300–150 m) **45.** Raunefjorden, Hordaland county (60°17′ N, 60–80 m). **43.** Rovdefjorden (62°12′ N, 200–150 m). **46.** Breisunddjupet (62°28′ N, 120–60 m), Møre og Romsdal county. **44, 47.** Tomfjorden, Nordland county (66°15′ N, 380–300 m). All specimens to scale, the largest (43) 4.2 mm diameter.

Anatoma crispata is smaller (2.25 vs. 5 mm), more globular, has a distinct funiculus, and more rapidly increasing whorls. The suture is adjacent to the selenizone of previous whorl. Teleoconch I has fewer and stronger axials. The shoulder is more convex with stronger, more irregular and strongly curved axials; spirals on the shoulder are fewer but more prominent, and with a wide adsutural sector devoid of spirals. The base has more widely spaced axials and spirals creating a grid with larger, almost square pits. The aperture has a less flaring lower and inner lip.

Anatoma schioettei is much smaller (2.15 vs. 5 mm) has a more elevated overall shell shape, has about half as many axials that are not crenulated, and the spirals are barely perceptible.

Anatoma schanderi is more turreted, has a protoconch with reticulate sculpture, the axials are much weaker, and about as strong as the spirals.

The radula of *A. tenuisculpta* differs from that of *A. crispata* mainly in having a broader rachidian tooth with 11 cusps, of which the central one is the longest, but is not isolated.

Type Material: Unknown whereabouts, presumed to be lost. **Neotype, here designated,** Terreti-Cellantoni Bridge, 567 m above sea level Pleistocene epibathyal facies, muddy clay, Italy, 38°07′ N, 15°43′ E (DLG 1421, 6), SBMNH 149680.

Type Locality: Pliocene/Pleistocene deposits near Reggio Calabria, southern Italy.

Other Material Examined: 92/80 specimens /shells of own material, 32/72 from the collections of ZMON, 22/38 from ZMBN, 3/12 from ZMTø and 7/0 from TBS. From other collections: Norway (NHMUK, 1): Dröbak, 59°40′ N, 10°38′ E (USNM 181590, 119; USNM 181591, 34; USNM 181589, 8); 60–130 m, Raunefjord, 60°16′ N, 5°09′ E (NMSZ 1973.59.1, 5); West of Ireland and Great Britain: 765 m, Rockall Trough, off W Scotland, 55°44′ N, 16°07′ W (NMR 993000033717, 32); 560 m, Rockall Trough, off western Scotland, 55°49′ N, 15°08′ W (NMR 993000033720, 6); 587 m, West of Rockall Trough, 55°30′ N, 15°48′ W (DLG 1217, 1); Southern North Atlantic: 621–786 m, Josephine Bank, Azores, 36°40′ N, 14°15′ W (USNM 181618, 1); 1920 m, Challenger Station SE342, 39°01′ N, 10°40′ W (NMSZ 1994128.60109, 8: complete); 1818 m, off W Portugal, 40°N, 9°15′ W (USNM 181602, 6); 2500 m, Challenger Station ES347, 41°38′ N, 11°20′ W (NMSZ 1994128.60110, 18: complete); 543m, Bahia de Cadiz, Spain, 35°30′ N, 6°08′ W (NMR 993000033757, 12); Mediterranean; 350 m, Fiumicino, Roma, 41°42′ N, 12° E (NMR ex 993000033735, 1); 400 m, Capraia, 43°03′ N, 9°54′ E (SRC, 1); 70–100 m, Northern Tyrrhenian Sea (SRC, 1). Palermo, 38°08′ N, 13°23′ E (ZMUC, 3).

Variability: In the Norwegian material the only signifieant variability seems to be differenee in shape (Figures 42–47). This is partly due to ehange with growth, older specimens always being taller than younger ones, but eomparison of shells in Figures 43 and 46 shows that shells of same size within a population may also differ. No geographieal trends in the Norwegian material are evident. Shells from the Mediterranean agree in all signifieant respects with the Norwegian material.

Distribution: The majority of records are from the eoast and fjords of Norway, but a few museum speeimens indieate that it can be found in moderately deep water (60–800 m) on the shelf and upper slope of the northeast Atlantic ocean, possibly from the Faroe Islands and southward to west of Gibraltar, with various deep-water loealities farther south. A very few reeords are from Italian waters, 70–400 m. The speeies is probably overrepresented in museum material from Norway beeause of its size. With a single exeeption, a few shells from Drøbak in Oslofjorden, all museum specimens are from western and northern Norway. In the material from ZMBN (22/38 speeimens/shells), records of *A. tenuisculpta* are from five to ten times more frequent than each of the other two inshore species. Our own material indieates that it is far less eommon in Norwegian waters than *A. crispata*, of whieh we have three times as many speeimens and six times the number of empty shells. The confirmed latitudinal distribution is from 67°10′ N, south to Korsfjorden (60°10′ N). The few shells from museum colleetions show that there is (or was) an isolated (?) population near Drøbak and scattered records north to Lofoten (68°25′ N) and southern Troms county (68°50′ N). The main depth distribution in Norwegian fjords is 80–200 m, with a few finds up to around 50 m (50–25 m dredge haul) and down to a little more than 300 m (380–300 m). A eouple of empty shells from a fjord bottom at 680 m indieate that it might have been living even deeper than 380 m.

Remarks: This is the speeies called *Anatoma* n. sp. in Høisæter (2009). Despite it having been figured and described repeatedly from Norwegian waters, the speeies has never been properly identified. This is partly due to the confusion surrounding *Scissurella angulata* Lovén, 1846, whieh was accepted by most authors as the name for this form, either as a full species or as a form of *A. crispata*. Lovén (1846) described but did not illustrate *Scissurella angulata* from northern Norway in a paper in which he also recorded *A. crispata* from Bergen. This indieates that he did observe differences that he regarded to be of specific value. His diagnosis in Latin (four lines) is not detailed enough to let us decide which of his two species is the real *A. crispata*. Luckily, one of two syntypes is in SMNH, and SEM of this specimen (Figure 18 above) elearly shows that what Lovén regarded as the new species *S. angulata* in fact is a specimen of *A. crispata*.

The speeies is thus in need of another name. *Anatoma richardi* (Dautzenberg and Fiseher, 1896), *A. josephinae* (Odhner, 1960), *A. umbilicata* (Jeffreys, 1883), and *A. tenuis* (Jeffreys, 1877) are all speeies deseribed from deep water (360–2650 m) in the North Atlantic. None of these names has ever been used for the "large" Norwegian speeies, and studies of the type material have eliminated all of them (Geiger, unpublished data). However, Seguenza (1877) deseribed three speeies of "*Scissurella*" from Pleistoeene/Plioeene deposits from the Reggio Calabria region in southern Italy (northern shore of the Messina Strait). Two of these, *S. tenuisculpta* and *S. argutecostata*, have shell morphologies indistinguishable from our Norwegian form. Later (Gregorio 1889), described a species, *S. funnazzensis* from 140–180 m depth off Sieily. Examination of his illustrations shows that this species is indistinguishable from Seguenza's two fossil "species". Warén (pers. eomm.) studied material of *S. tenuisculpta* from the type loeality (any types have most likely been destroyed during one of many earthquakes in the region during the first half of the last eentury; Warén, 1980) and eonsiders specimens from these deposits indistinguishable from Reeent specimens from Mediterranean and Norwegian waters. We agree and apply the first reviser's prineiple in selecting *tenuisculpta* as name for the speeies. We eautiously apply this speeies epithet to the Norwegian material. We designate here a **neotype** (Figure 34) for *A. tenuisculpta* with the explicit intention of taxon stabilization.

Starting with Jeffreys (1865), many authors have regarded Lovén's *A. angulata* as a variety of *A. crispata*, "As I suspected, *S. angulata* of Lovén is a large form of this species [*A. crispata*]" (Jeffreys 1870: 444). Jeffreys, familiar with the British forms of *A. crispata*, got acquainted with the large Scandinavian "variety" on a dredging excursion to Oslofjorden (Drøbak), and probably assumed that the form described as new by Lovén was this large form. Friele (1874), G.O. Sars (1878), Norman (1879, 1893), Sehneider (1886) all accepted *A. angulata* as a form or variety of *A. crispata* (mostly implieitly as they did not neeessarily mention *A. angulata*, although, judging from museum material, they certainly were mainly studying *A. tenuisculpta*). Both G.O. Sars (1878), and Norman (1893) remarked that the Norwegian form of *A. crispata* attains a much larger size than the British form of the species. Norman did not mention Lovén's speeies, but G.O. Sars followed Jeffreys and synonymized both *A. aspera* and *A. angulata* with *A. crispata*, and even ventured the fanciful hypothesis that the British specimens studied were all juveniles. Monterosato (1890), in his survey of the molluses of the depths of the waters of Palermo, diseussed both *S. tenuisculpta* and *S. angulata*, the latter based on the deseription and illustration in G.O. Sars (1878). Monterosato left no doubt that he regarded the large form from Norway as a species separate from *A. crispata*, and that it should be identified

as *S. angulata* Lovén. He compared the fossil, *S. tenuisculpta* with *S. affinis* O.G. Costa (which he synonymized with *S. funnazzensis* de Gregorio, 1889) and consequently regarded (Monterosato, 1890: 143) the large Norwegian species ("The largest European species and probably the largest known species, living or fossil, confused by all with *S. crispatus*") as distinct from *S. tenuisculpta*. The only comment on *S. tenuisculpta* is its "restricted umbilicus".

The first author to seriously discuss the relationship between the three forms from Scandinavia was Odhner (1912: 13), who provided the following description of *Scissurella crispata* var. *angulata*: "Shell less depressed (than *S. crispata* s.s.); whorls more flattened above; body-whorl therefore more angulated; aperture = 2/3 the spire; H. 4.2, D. 5 mm; whorls 4 3/4 - var. *angulata* Lovén, 1846." This description undoubtedly refers to our *A. tenuisculpta*. Odhner, however was not consistent in his concepts of *"angulata"* and *"crispata"*. In Odhner (1960) he again referred to *A. crispata* var. *angulata* when describing his species *A. josephinae*. By including specimens from Trondheimsfjorden and Bohuslän (western Sweden) under the var. *angulata* umbrella, he demonstrates that his idea of the variety was not in accordance with *tenuisculpta*. Lovén's original material from "Finmark" (might be from anywhere in northern Norway, not necessarily in Finnmark county) consisted of two specimens (the only remaining shell is designated by us as **lectotype**, illustrated in Figure 18 above), both of which were studied by Odhner (1912); Lovén gave the maximum diameter as 2.4 mm (corresponding height 1.8 mm), quite different from the 5 mm he gave as the diameter in the diagnosis for *A. crispata* "var. *angulata*."

In more recent literature from the northeastern Atlantic, several illustrations of *A. crispata* are based on *A. tenuisculpta*. This is also true for the drawing in Hubendick and Warén (1974) from the Bergen area, western Norway, and the one in Fretter and Graham (1976) and thus also Graham (1988), which is the drawing by Poul Winther based on another shell from the Bergen area. Fretter and Graham (1976) also presented two SEM images of the spire of what is actually a specimen of *A. tenuisculpta* from the Bay of Biscay.

In Norway, *Anatoma tenuisculpta* is often found (alone or with *A. crispata* and/or *A. aspera*) at intermediate depths, from 50 m downwards, at least down to 460 m (Trondheims-fjorden; Norman, 1893). The substrate varies, but when a mixture of silt, shell gravel and small stones (and often with an abundance of *Modiolula phaseolina*) is present, the chances of finding this species are good. As late as June 2010, eight specimens were found in outer Korsfjorden (60°08′ N, 255–289 m). The depth distribution of the three species is discussed further in the Discussion below.

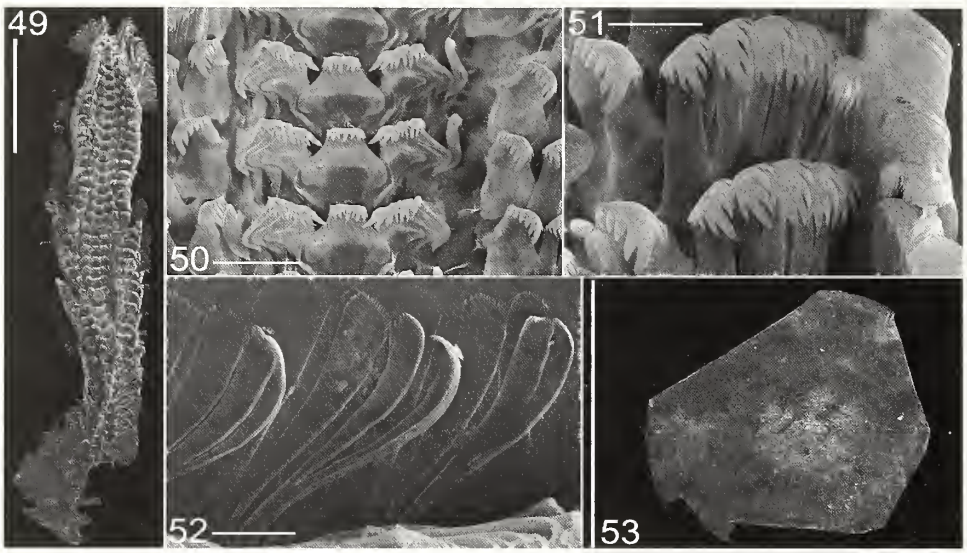
Anatoma schioettei new species

(Figures 48–60)

Description: (Largely based on holotype, Figure 48). Shell of moderate size (to 2.15 mm diameter), trochiform, stepped. Protoconch of 0.75 whorls, loose flocculent sculpture with some of the flocculae organized into a distinct spiral on top of protoconch and another, smaller and indistinct spiral near the inner part of the protoconch. No apertural varix, apertural margin straight, clearcut. Teleoconch I of ca. 0.75 whorl, with approximately 15 axial cords, (weak) spiral cord in position of selenizone. Teleoconch II of up to 2 whorls, suture one to two selenizone widths below selenizone. Shoulder slightly convex, strong axial cords, approximately 30–35 on first teleoconch II whorl. Weak spiral threads starting late, with a single thread increasing gradually to three to five near aperture. Base with same axial sculpture as on shoulder, 30–55 per whorl, one out of five or six fading out near middle of base. Around 16 weak spiral cords on base, getting gradually weaker towards the periphery. Umbilicus open, wide, distinct narrow funiculus. Aperture rounded oblong. Selenizone at periphery, keels moderately elevated, weak.

Radula (Figures 49–53): Rachidian tooth trapezoid, central cusp largest, four cusps in arc on each side of tip. Lateral teeth 1–3 similar, apical cusp largest, 4–5 progressively smaller cusps on outer edge of tip. Lateral tooth 4 reduced, hook-shaped, with 1–2 cusps on outer edge. Lateral tooth 5 enlarged, apical cusp largest, 6–7 cusps along inner edge, 2–3 along outer edge. Inner marginal teeth with triangular tip, apical cusp largest, 4–5 cusps on each side of tip. Outer marginal teeth with spoon-shaped tip, many small cusps along edge. Outermost marginal teeth paddle-shaped with many fine bristles along tip. Radular interlock of central field moderate.

Figure 48. *Anatoma schioettei* new species, holotype, SEM, from 749–774 m, off Greenland, 75°01′ N, 12°38′ W (ZMH K–42704), 2.15 mm diameter. Scale bar shell = 1 mm; Scale bar protoconch = 100 µm.



Figures 49–53. *Anatoma schioettei* new species, 2.15 mm diameter, radula and operculum. Specimen from 749–774 m, Greenland, 75°01′ N, 12°28′ W (ZMH K–42705). **49.** Entire radula. Scale bar = 200 µm. **50.** Central field. Scale bar = 20 µm. **51.** Lateral tooth 5 and marginal teeth. Scale bar = 10 µm. **52.** Outermost marginal teeth. Scale bar = 10 mm. **53.** Operculum. Scale bar = 1 mm.

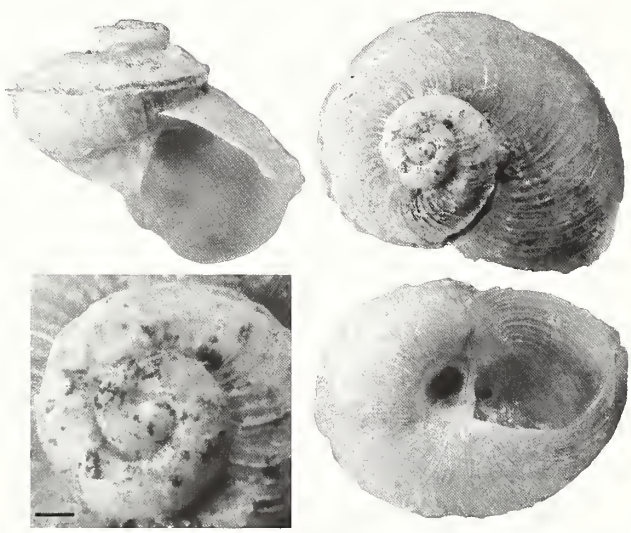


Figure 54. *Anatoma schioettei* new species, Trollveggen vent field just north east of Jan Mayen, 71°18′ N, 5°47′ W, 574 m, 1.95 mm diameter. Scale bar protoconch = 100 µm.

Differential Diagnosis: *Anatoma crispata* has whorls that are closer to the selenizone of the previous whorl, has at least twice as many axials, crossed by stronger spirals, and has a more narrow umbilicus.

Anatoma tenuisculpta is much larger (5 vs. 2.15 mm), has suture closer to the selenizone of the previous whorl, has at least twice as many axials, which have a crenulated appearance due to the crossing spirals, and lacks a funiculus.

Anatoma aspera has a taller overall shell, has stronger axials on the shoulder, and lacks a funiculus.

Anatoma schanderi has a taller shell with the base visible between suture and selenizone at an angle towards the spindle, is much larger (4.5 vs. 2.15 mm), spirals and axials of approximately equal strength, and a protoconch with more regular net sculpture.

The radula of *A. schioettei* is similar to the one of *A. crispata*, narrow necked rachidian with an isolated central cusp with three smaller cusps on each side. Lateral teeth 1–3 similar, each with three strong cusps. Lateral tooth 4 narrow with only one cusp. Lateral tooth 5 wide with at least seven cusps of which no. six from center is the strongest.

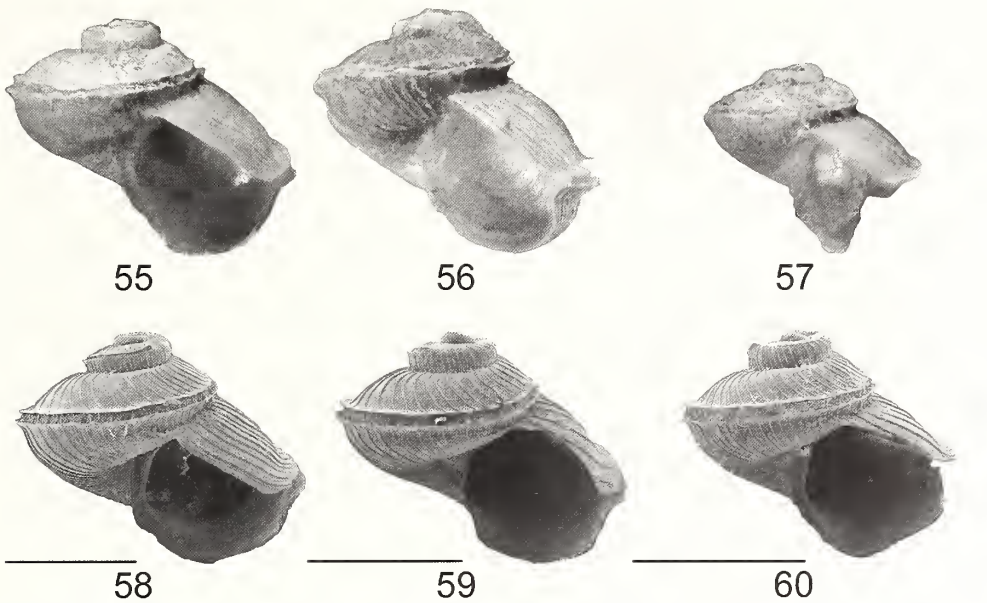
Type Material: Holotype, ZMH K 42704, Paratypes ZMH K 42705–42710, ZMUC GAS–427, 428.

Type Locality: 749–774 m, upper slope off East Greenland, 75°01′ N, 12°38′ W.

Other Material Examined: Three specimens from 574 m, H2Deep ROV dive 22-2008, the Trollveggen vent field just NE of Jan Mayen, 71°18′ N, 5°47′ W; 70 m, Greenland, 76°33′ N, 69°23′ W (ZMUC, 3: complete); 100–110 m, Greenland, 76°33′ N, 69°0′ W (ZMUC, 1: complete); 197–198 m, Greenland, 75°01′ N, 13°48′ W (ZMUC, 1, 1: complete) (ZMUC – GAS – 427, 428).

Etymology: Named after Tom Schiøtte of ZMUC. He generously provided material that he had been working on himself, which provided the radulas for the two new species.

Variability (Figures 55–60): Number and density of axials vary, as does the presence or distinctness of spirals on the shoulder, normally three but sometimes five weak spirals are present on the middle of the shoulder. The



Figures 55–60. *Anatoma schioettei* new species, six specimens from the northern Norwegian Sea. **55–57.** Three (LM) from the Trollveggen vent field, 574 m. **58–60.** Three (SEM) from the upper slope off northeast Greenland, 749–774 m (ZMH K – 42705–42710.). Scale bars all = 1 mm.

spirals are always much weaker than the axials, and at times only visible under very high magnification.

Distribution: The main distribution, judged by the limited material available, appears to be the shelf and upper slope off northeast Greenland, but as the two records from northern Baffin Bay show, it probably has a wide distribution in Arctic waters. As shown below, variants of the species may extend to "shallow" water hot vents near Jan Mayen, and to the upper slope off western Norway (ca. 62° N).

Remarks: Two "forms" of this species appear to be present in the Norwegian Sea, one on the upper slope off Greenland, at a depth from around 70 to 750 m at 75° N (Figures 58–60), the other one at the "Trollveggen" vent locality just northeast of Jan Mayen at 71°18′ N, at 574 m (Figures 54, 55–57). The main shell differences appear to be erosion and deposit of dark brown and black particles (microbes?) on shell surface.

In contrast to other known vent faunas, the vent faunas on the two investigated vent fields in the Norwegian Sea seem to be recruited from the surrounding soft bottom. Thus, two or three species of the skeneid gastropod *Skenea* are very similar to upper slope species on the "Trollveggen" hot vent, while the single *Skenea* species found on a much deeper hot vent locality in the same area, is similar to a species living on the adjacent soft bottom (Høisæter, unpublished). Whether or not the two "forms" are distinct species is impossible to ascertain from our material, but these subtle morphological similarities make it hard to support description of two new species (see the discussion below on why we accept *A. aspera* and *A. tenuisculpta* as Recent species although based on fossil types.) *Anatoma* spp. are not unknown from hot vent environments, as shown by the Japanese *A. fujikurai* Sasaki, Geiger and Okutani, 2010.

Anatoma* cf. *schioettei
(Figures 61–67)

Anatoma crispata (in part): Høisæter 2009: 21; 2010: 240, fig. 6A.

On the upper slope off Norway, an *Anatoma* (Figures 61 and 62) was found that was originally classified as a somewhat deviant "form" of *A. crispata* (see Høisæter 2010). Altogether four specimens and seven shells of this form were found in a dredge haul from 543 m and one specimen from 602 m, presumably from sandy/muddy sediment. On closer inspection (especially from SEM illustrations), the specimens turned out to be more similar to *A. schioettei* than to *A. crispata*. This similarity is based on a turreted and rather lenticular shell shape, and a protoconch that is pretty similar in the two forms. The protoconch is scattered with small irregular flocculae that merge onto a continuous spiral line on top of the protoconch in both forms. In addition the protoconch is in both cases terminated in a clean, straight apertural margin. This as opposed to the single irregular varix in *A. schanderi*, the "double" varix in *A. aspera* and the gradual transition between the two parts of the shell in *A. crispata*.

The main difference from *A. schioettei* sensu stricto is the strength of the axials, which can be variable in other species. Radulae are similar but the number and shape of the cusps on the rachidian and the laterals are different, *A.* cf. *schioettei* have more cusps on each tooth, and the cusps are generally less pointed than those of

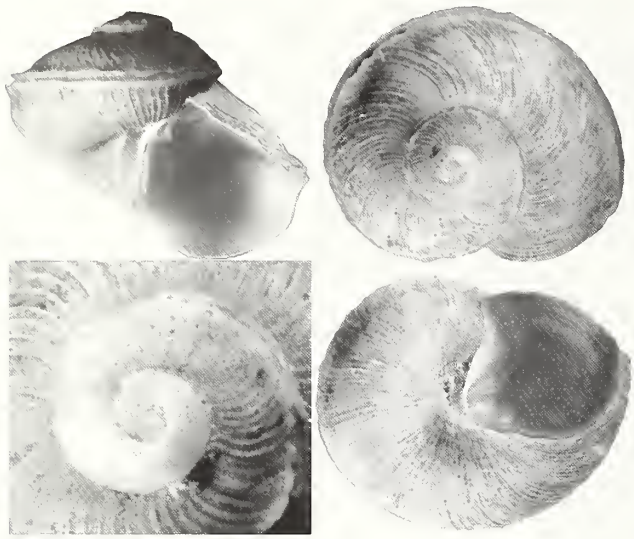


Figure 61. *Anatoma* cf. *schioettei* from upper slope off the Norwegian Trough, 62°20′ N, 543 m, 2.4 mm diameter. Scale bar = 200 µm.

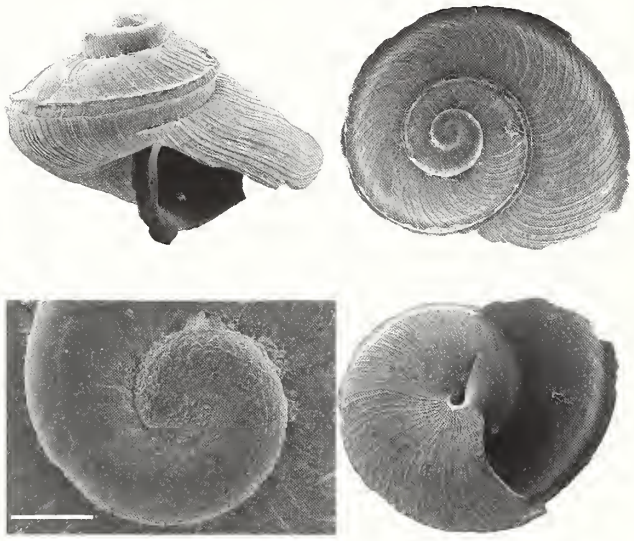


Figure 62. *Anatoma* cf. *schioettei*, upper slope off the Norwegian Trough, 62°20′ N, 543 m, 1.7 mm diameter. Scale bar = 100 µm.

A. schioettei. That this aberrant form have supernumerary lateral teeth (six instead of five) might be just an individual aberration.

Remarks: The distribution of this form is far from the known distribution of *A. schioettei* sensu stricto. The upper slope off Norway has a gastropod fauna apparently heavily influenced by the fluctuating temperature of the bottom-near water (Høisæter, 2010). The relationship of the fauna is with conspecifics or closely related species on the Faroe-Shetland Ridge or on the shelf/upper slope north of the Faroes. In this case the shelf/slope off Greenland, both East and West Greenland, also seems to be inhabited with a species closely related to a species from the upper slope off Norway.

***Anatoma schanderi* new species**
(Figures 68–83)

Description: (Largely based on holotype, Figure 68). Shell fragile, of medium to large size (to 4.5 mm diameter), trochiform, biconical, stepped. Protoconch of 0.75 whorls, reticulate sculpture (Figure 69), with distinct apertural varix, apertural margin straight. Teleoconch I comprising almost a full whorl, with approximately 30 axial cords, strong spiral cord in position of selenizone. Teleoconch II of up to 2.5 whorls, suture lightly impressed, well separated from selenizone by ca. 2 widths of selenizone (Figures 69 and 83). Shoulder convex, numerous and fairly weak axial cords, approximately 65–70 per whorl in fully grown specimens. Four to five rather indistinct spiral threads on middle of shoulder. Basal sculpture dominated by strong, widely spaced spiral cords, sometimes getting more conspicuous towards umbilicus, crossed by fine axial threads (Figures 68 and 69). Most axial threads fade away towards umbilicus, but 10–12 strong spiral cords continue into it (Figure 69). Umbilicus open, wide; funiculus narrow, indistinct. Aperture rounded-oblong, baso-adumbilical region flared. Selenizone slightly above periphery, keels of moderate strength.

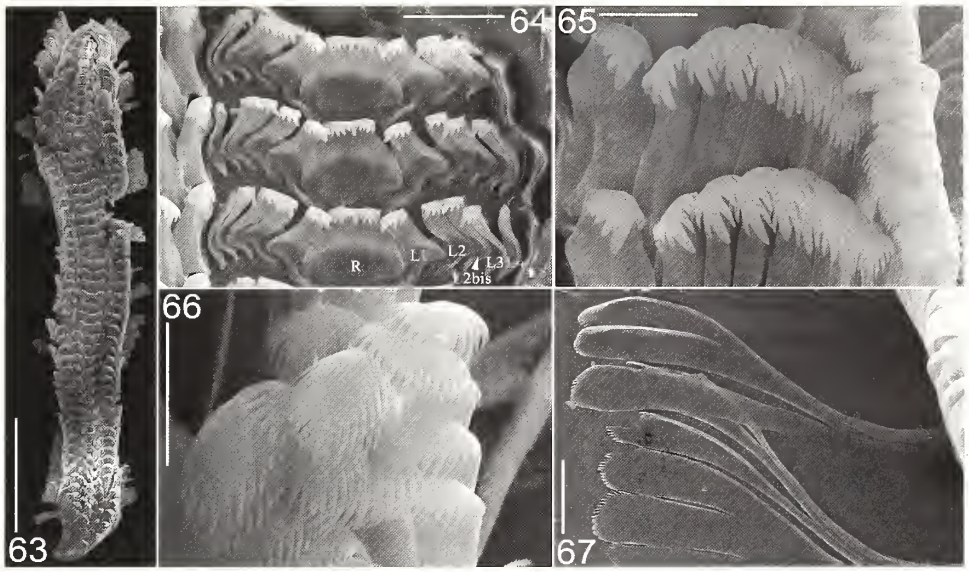
Radula (Figures 70–75): Rachidian tooth trapezoid, central cusp largest, 7–8 cusps in straight line on each side. Lateral teeth 1–3 similar, apical cusp largest, 4–5 cusps along outer edge of tip. Lateral tooth 4 reduced, hook-shaped. Lateral tooth 5 enlarged, apical cusp largest, 5–6 cusps along inner edge, 3–4 cusps along outer edge of tip. Inner marginal teeth with oval tip, apical cusp largest, 6–10 cusps along each side. Outer marginal teeth with spoon-shaped tip, many fine bristles along edge. Outermost marginal teeth paddle-shaped, with many fine bristles along tip. Radular interlock of central field moderate.

Differential Diagnosis: *Anatoma crispata* is smaller than *A. schanderi* (2.25 vs. 4.5 mm), has more pronounced axial sculpture, has a distinct funiculus, and the protoconch has flocculent sculpture.

Anatoma aspera is smaller (3.3 vs. 4.5 mm), has a taller, more turreted shell, and has much stronger axial sculpture on the shoulder.

Anatoma tenuisculpta grows somewhat larger (5.5 vs. 4.5 mm), has an overall more disc-shaped shell, and the axials are stronger with a crenulated appearance due to the crossing spirals.

Anatoma schioettei is much smaller (2.15 vs. 4.5 mm) has much more distinct axials, and the protoconch has flocculent sculpture.



Figures 63–67. *Anatoma* cf. *schioettei*, radula from specimen in Figure 62. **63.** Entire radula. Scale bar = 1 mm. **64.** Central field enlarged. Scale bar = 100 µm. **65.** Inner marginal teeth. Scale bar = 20 µm. **66.** Outer marginal teeth. Scale bar = 10 µm. **67.** Outermost marginal teeth. Scale bar = 20 µm.

Type Material: Holotype ZMBN 87296; four paratypes ZMBN 87297–87298.

Type Locality: The southern margin of the Greenland Basin (73°34′ N, 7°50′–8°01′ E) in the Norwegian Sea, 2560–2580 m. In a sample of semi-lithified sediment. (H2Deep ROV sample 7-2008.)

Other Material Examined: A fragment from H2Deep ROV Dive 1, 2430 m, near the Schultz Massif, 73°39′ N, 07°47.5′ E; 1509–1525 m, off eastern Greenland, 74°54′ N, 12°30′ W (ZMUC, 20); 749–774 m, Greenland, 75°01′ N, 12°38′ W (ZMUC, 20); 120 m, 10–15 km NW of Digby Neck, Nova Scotia, Canada, 44°36′ N, 65°45′ W (JWC 7286, 1).

Etymology: Named after Professor Christoffer Schander from the University of Bergen, who recognized the significance of what now are the type specimens during sorting of material.

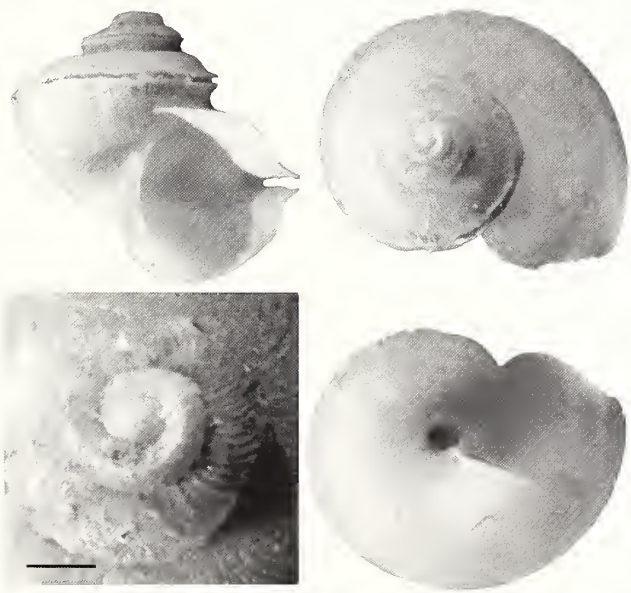
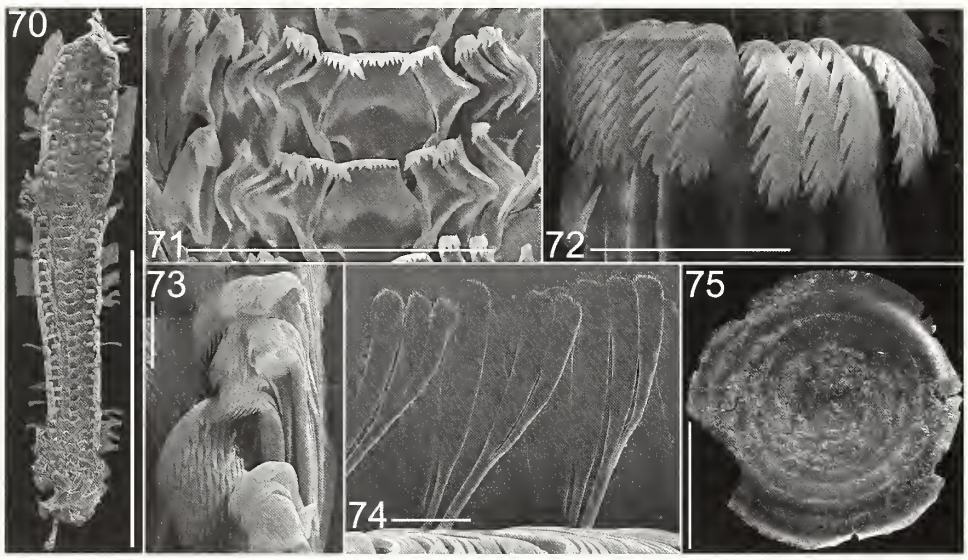
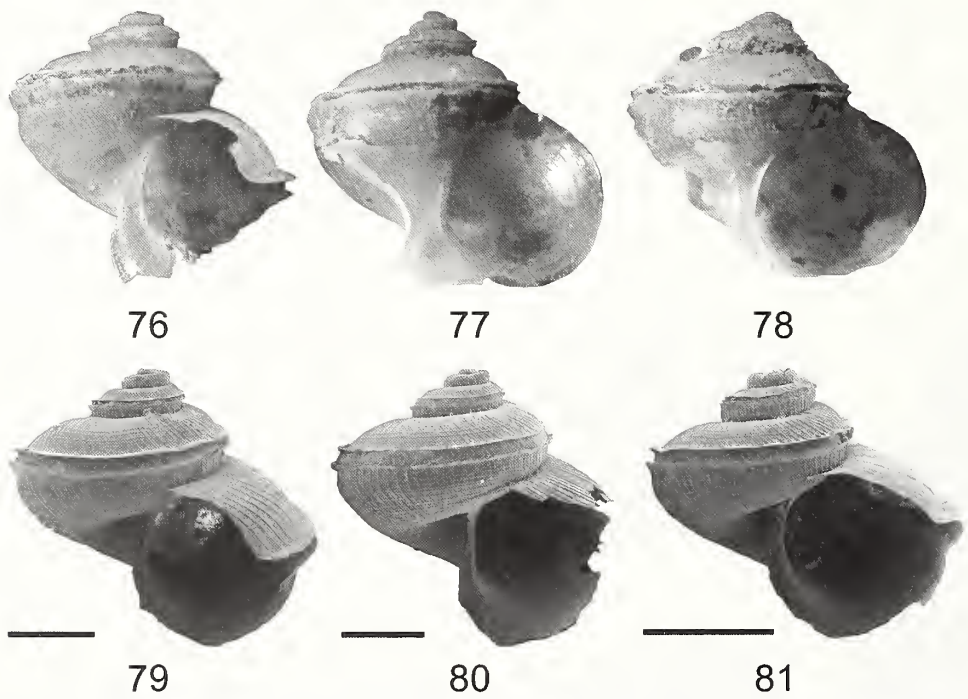


Figure 68. *Anatoma schanderi* new species, holotype (ZMBN 876296), southern margin of the Greenland Basin, 73°34′ N, 7°50′–8°01′ E, Norwegian Sea, 2560–2580 m, 2.5 mm diameter. Scale bar protoconch = 200 µm.

Figure 69. *Anatoma schanderi* new species, off eastern Greenland, 74°54′ N, 12°30′ W (ZMUC, 20), 1509–1525 m, 4.4 mm diameter. Scale bar shells = 1 mm; Scale bar protoconch = 100 µm. Radula shown in Figure 70.



Figures 70–75. *Anatoma schanderi* new species, radula and operculum from specimen shown in Figure 69. **70.** Entire radula. Scale bar = 1 mm. **71.** Central field enlarged. Scale bar = 100 µm. **72.** Inner marginal teeth. Scale bar = 20 µm. **73.** Outer marginal teeth. Scale bar = 10 µm. **74.** Outermost marginal teeth. Scale bar = 20 µm. **75.** Operculum. Scale bar = 1 mm.



Figures 76–81. *Anatoma schanderi* new species, **76–78.** Three paratypes from the southern margin of the Greenland Basin, 73°34′ N, 7°50′–8°01′ E, in the Norwegian Sea, 2560–2580 m. **79–81.** Three specimens from the slope off East Greenland, ca. 1520 m. Scale bars = 1 mm.

Variability (Figures 70–75): Due to their fragility, the deep water paratypes are all poorly preserved, but what remain of the shells indicate that the variability is slight. Material from most other localities seems to fall within the range of variation of the type material. Only the relative strength of axials and spirals on the base varies somewhat. The selenizone of the specimen from Canada (see below) is wide and with a very narrow keel, and the shell is also more globular than the rest. It is impossible to tell if this is of taxonomic importance however (due to geographical isolation or just individual variation).

82 83

Figures 82–83. *Anatoma schanderi*, top whorls. **82.** Paratype in Figure 76. **83.** Specimen from the slope off Eastern Greenland, ca. 1520 m. Scale bars = 200 µm.

Distribution: Except for the single record from 120 m, Nova Scotia, Canada all material of this species are from rather deep water (750 to ca. 2600 m) in the Greenland Sea (the northwestern part of the Norwegian Sea.) The record from Canada indicates that the species has a mainly northwest Atlantic distribution, rather than being a purely deep water form.

Remarks: The reticulate pattern on the protoconch would have placed this species, according to the accepted generic taxonomy, in the genus *Thieleella* Bandel, 1998. For the purpose of this revision, we have decided to include *Thieleella* as a synonym of *Anatoma*. Figures 82–83 shows the uppermost whorls of two shells, LM photo at left and SEM photo at right. It illustrates that in spite of the lack of microscopic details in the LM photo, it is still possible to recognize some of the most important distinguishing characters without using SEM imaging.

Anatoma umbilicata (Jeffreys, 1883)

Scissurella umbilicata Jeffreys, 1883: 88–89, pl. 19, figs. 1–1a.

In Høisæter (2009) *Anatoma* cf. *umbilicata* is listed representing a specimen from the Norwegian Sea deep slope just north of the Faroes at 2222 m. The shell was very deteriorated and not suited for photography. In view of the presence of *A. schanderi* in this general area, the determination is quite dubious and needs verification.

Anatoma umbilicata is a mostly misidentified species. For instance, Sabelli et al., (1990), Gianuzzi-Savelli et al. (1994), and Adrovini and Cossignani (1999) record *A. crispata* and *A. umbilicata* as the only two species from the Mediterranean. The latter two references present respectively good quality SEM images and photographs, which make clear that both species were misidentified. We base our species concept of *A. umbilicata* on all extant type material examined by SEM (DLG, unpublished data).

DISCUSSION

After Geiger started looking closer at details on shells of Anatomidae from various parts of the world (Geiger, 2003; Geiger and Jansen, 2004a, b; Geiger, 2006a; Zelaya and Geiger, 2007; and Geiger and MacLean, 2010), it has become increasingly evident that the supposedly wide ranging *A. cristata* is a complex of several species. As demonstrated above, the complex is represented by three species in inshore Norwegian waters. The naming of these three species has not been straightforward though, as a number of early names, subsequently partly relegated to synonymy, are available for the species. *Anatoma crispata* was described from beach drift after a storm on small Noss Island just outside Lerwick on Shetland (Jeffreys, 1865: 285). Comparison with specimens from Shetland and our selection of neotypes have provided convincing arguments for assigning this name to the smallest of the three Norwegian species. For one of the remaining two species we have accepted the previously introduced name of a Pleistocene/Pliocene fossil from southern Italy, and for the last one we have resurrected the name of another fossil from about the same deposits.

The allocation of Recent specimens to species previously known only from the fossil record is always a tricky matter, and, when as in this case, the number of recorded specimens from the intervening localities (between the Mediterranean and Norway) is limited, this is even more problematic. There are examples in which extant marine species are known to have survived morphologically unaltered since the Pleistocene (and even the Pliocene, i.e., more than two million years). In Anatomidae, such an example is *Anatoma lyra* (Berry, 1947) described from the lower Pleistocene of Los Angeles, California, USA. Its holotype is indistinguishable from Recent material at the SEM level, including live-collected specimens (DLG, unpublished data). The synonymy of Mediterranean Pleistocene fossils with Recent North European inshore species represent a special case. As the various glacials forced boreal species living in the fjords of Norway in the warmer interglacials, to migrate south along the European shelf and slope, some of them were trapped in the Mediterranean, where they today are known as Pleistocene fossils. Some, but not all, succeeded in migrating north again to Norwegian waters when water temperatures increased, while others remained in the Mediterranean and evolved into "sister" species. Which of the fossils are genetically similar

enough to be regarded as conspecific with the forms today living in Norwegian fjords is an open question, but as long as there are Recent specimens both in the Mediterranean and in Norway, the question might be settled by molecular genetic investigations. If there is a continuous distribution of the morphospecies from Norway to the Mediterranean Sea close to the fossil deposits, this might also be a reasonable justification for accepting the name of the fossil. Those conditions seem to be met both with *A. aspera* and *A. tenuisculpta*.

Anatoma aspera has been accepted, mostly as a variety of *A. erispata*, by most modern authors as a form or species with a mainly south European distribution. Further research might demonstrate that differences between the Mediterranean and the north European populations are of a magnitude necessitating specific separation, in which case the name *A. paucicostata* (Jeffreys, 1865) is available. About the same argument holds for *A. tenuisculpta*, but in this case no synonym based on Recent material from the North Atlantic is available.

Within Anatomidae, recently elevated to full family rank (Geiger and Jansen, 2004a; Geiger 2006a), three genera, *Anatoma* Woodward, 1859, *Thieleela* Bandel, 1998, and *Sasakieoneha* Geiger, 2006 have been accepted by Geiger and collaborators (e.g., Geiger 2006b; Geiger and McLean, 2010; Zelaya and Geiger, 2007) as well as some other authors (e.g., Marshall, 2002). Of these, *Anatoma* and *Thieleella* are distinguished by a single character, the microsculpture on the protoconch, invisible except under very high magnification (i.e. under SEM). Thus *Thielleella* is characterized by a reticulate pattern, while *Anatoma* is either smooth or with flocculent pattern. Of the five species treated here, *A. schanderi* has a typical *Thieleella* reticulate pattern, while both *A. crispata* and *A. tenuisculpta* have protoconchs with very dense flocculation. *Anatoma schioettei* and *A. aspera* have protoconch microsculpture somewhat intermediate between these extremes, with a very open flocculation where some of the flocculae link together in an irregular reticulation (Figures 22 and 48). For the purpose of this revision we therefore include *Thieleella* as a synonym in *Anatoma*. This is done mainly for practical reasons, as specimens studied only by LM or specimens with worn protoconchs are impossible to place in the correct genus if the *Anatoma*/*Thielleella* dichotomy is retained.

The species of *Anatoma* all seem to occupy specific microhabitats although they often occur together in sledge or dredge hauls. Thus two of the inshore species co-occur in several samples and all three inshore species have been found together (alive) in two of our samples from western Norway. *Anatoma crispata* is found all around the Norwegian coast (and beyond), in depths from 10 to at least 200 m inshore (at least to 1000 m on the upper slope), and in temperatures from +12°C to −1.4°C. It appears to be associated with clean, hard bottom habitats and is often (in Norwegian waters) accompanied by species such as *Gibbula tumida* (Montagu, 1803), *Margarites striata* (Leach, 1819), *Lacuna vincta* (Montagu, 1803), and *Pusillina inconspicua* (Alder, 1844).

Anatoma aspera is found occasionally in waters not deeper than 40 m, it has its main distribution in depths between 60–100 m, but with records also from dredge hauls taken from 260 to 180 m. The conspicuous break between 64°40′ N and 69° N in the otherwise largely continuous distribution along the coast may provide support for the theory that *A. aspera* is mainly a southern species, having invaded the Norwegian coast at around 63° N and from there spread northward and southward. The shells (not in very well preserved condition, Figures 30 and 33) found at 69°14′ N at the considerable depth of 370 m, might be remnants of a separate invasion farther into the north. *Anatoma aspera* is (in Norwegian waters) most often found in, or near hypoxic, blackish mud, and is often found accompanied by *Puncturella noachina* (Linné, 1771), *Melanella lubrica* (Monterosato, 1890), *Troplionopsis barvicensis* (Johnston, 1825), and several pyramidellids, especially *Chrysallida eximia* (Jeffreys, 1849).

Anatoma tenuisculpta is the inshore Norwegian species living deepest, being usually found between 150–300 m, but with occasional records from 50 m and as deep as 500 m. This seems to agree with the known distribution (based on scattered museum material) along the lower shelf/upper continental slope of the northeast Atlantic, from the Faroes south to Gibraltar. *Anatoma tenuisculpta* is (in Norwegian waters) most commonly found on mixed bottoms often with some shells of *Modiolula phaseolina*, silt and shell gravel. Common accompanying gastropods are *Trophonopsis barvicensis* (Johnston, 1825), *Teretia teres* (Reeve, 1844), *Spirotropis modiolus* (de Cristofori and Jan, 1832) and (in the Møre og Romsdal part of the distribution) *Solariella amabilis* (Jeffreys, 1865).

Except for its part-time association with hot vent habitats, *A. schioettei* seems to be most common in upper slope habitats in the western part of the Norwegian Sea, at depths of 200–800 m. The bottom substrate is presumably silt or ooze, and the temperature is probably fluctuating between positive and negative values. The only Anatomidae known from hot vents in the Norwegian Sea most likely belong to this species as well. *Anatoma schanderi* has (with a single exception, see above) so far only been found in the bathyal parts of the Norwegian Sea, from 1500–2600 m, where the bottom substrate may be semi-lithified and the temperature is constant at −0.9°C.

The conclusion in Geiger and Sasaki (2009) that no members of Scissurellidae occur in these northern latitudes, neither in shallow nor in deep water, is supported by this revision. The five species of *Anatoma* are, on the other hand, nicely distributed on various depth zones so that the whole depth spectrum seems to be occupied by this family of gastropods.

The large majority of museum-material from south of 62° N in Norway belong to *A. tenuisculpta*. This may be

partly because this species is appreciably larger than the other two species, especially *A. crispata*, but we regard it as unlikely that this should be the only reason. Thus we conclude that this species is (or has been) the main representative of the genus in western Norway, becoming gradually less common further north along the coast. It is not known from the Norwegian south coast or the Swedish west coast (A. Warén, pers. comm.). (A notable exception is the occurrence of *A. tenuisculpta* at Drøbak in Oslofjorden).

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A new species of *Praticolella* (Gastropoda: Polygyridae) from northeastern Mexico and revision of several species of this genus

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ABSTRACT

A new species of polygyrid land snail of the genus *Praticolella* from northeastern Mexico is described. This species has established invasive populations in the United States and Caribbean and has been confused with *P. griseola* and *P. berlandieriana*. The new *Praticolella* species is similar to *P. griseola*, but differs in being larger, having a more robust, depressed shell with white pigmentation, a flattened wide body whorl, and a more oval-shaped aperture. The range of these two species does not appear to overlap with *P. berlandieriana*, which is restricted to central, north, and east Texas. These two species are also circumscribed and their taxonomic history is reviewed. This new taxonomy was established using mitochondrial 16S rDNA and cytochrome c oxidase subunit-I sequences as well as geometric morphometric examination of the shells of each species.

Additional keywords: Mollusca, Invasive species, snail, mitochondrial DNA analysis, mitochondrial 16S rDNA, cytochrome c oxidase, geometric morphometric analysis

INTRODUCTION

Praticolella von Martens, 1892 is a genus of polygyrid land snails found throughout the southeastern United States (USA), Mexico, and South to Central America (Pilsbry, 1940). *Praticolella* is currently composed of 15 recognized species (Pilsbry, 1940; Hubricht, 1984), nine of which are species of conservation concern having global heritage ranks of G1, G2, or G3, indicating they are considered critically imperiled, imperiled, or vulnerable (Master, 1991; NatureServe, 2005). This paper aims to distinguish among several morphologically similar species of land snail in the genus *Praticolella*.

Species in *Praticolella* possess highly variable morphological characteristics often used in their taxonomy: the openness of the umbilicus; degree of depression of the spire; and the pattern of pigmented bands on the shells. This has led to disagreements about taxonomy of species in the genus (von Martens, 1890–1901; Singley, 1893; Pilsbry, 1940; Cheatum and Fullington, 1971; Neck, 1977; Hubricht, 1984). The last taxonomic revision of the United States species was by Pilsbry (1940) but excluded the five nominal Mexican taxa; these Mexican taxa were last revised by von Martens (1890-1901).

Praticolella griseola (Pfeiffer, 1841) is the only member of the genus currently considered to be introduced or invasive in the United States (USA) (Dundee, 1974; Robinson, 1999). Individuals identified as *P. griseola* have been recorded in the southeastern USA and the Caribbean since the 1920s. In addition, the United States Department of Agriculture (USDA) routinely intercepts *P. griseola* traveling with shipping trade.

This paper provides the means to distinguish several morphologically similar species of *Praticolella*, at least two of which regularly travel with shipments of fruit and greenhouse plants. The data presented here will make evident that other *Praticolella* species also need taxonomic attention, but this paper focuses on *P. griseola* and the species which must be considered to sort out the taxonomy of the invasive *Praticolella* species. These include: *P. griseola*, *P. berlandieriana* (Moricand, 1833), and *P. strebeliana* (Pilsbry, 1899). In this study, I use 16S rDNA (16S) and cytochrome c oxidase subunit I (COI) mitochondrial DNA and shell geometric morphometric analysis to provide the basic taxonomic and phylogenetic information necessary for taxonomy, conservation, and management of these invasive mollusks and native congeners.

MATERIALS AND METHODS

Table 1 lists specimens examined for DNA analysis, collection sites, latitude and longitude, and museum accession numbers of all specimens (also shown in Figure 1). Specimens examined in this study are deposited in the Academy of Natural Sciences of Philadelphia. Additional specimens for morphometric analysis (also listed in Table 1) were borrowed from the Florida Museum of Natural History, Gainesville; American Museum of Natural History, NewYork; Museum d'Histoire Naturelle, Geneva; and Field Museum of Natural History, Chicago.

Table 1. Locality information and museum number for specimens sequenced for DNA analysis followed by locality information and museum number for additional lots included in morphometric analysis. In these additional lots all adult, complete shells were photographed and included in morphometric analysis. ANSP numbers beginning with "A" represent lots preserved in alcohol. Latitude and Longitude presented in decimal degrees.

Species	Locality	Museum Number	Latitude	Longitude
Localities for DNA specimens				
Praticolella berlandieriana	9 km N New Braunfels, Comal Co. TX	ANSP A22076, ANSP 426024	29.7739	–98.1601
Praticolella berlandieriana	12.6 km SE of Blanco, Blanco Co. TX	ANSP A22079	30.0204	–98.3300
"Praticolella griseola" Cameron Co	Point Isabella high school, Port Isabel, Cameron Co. TX	ANSP A22074, ANSP 426021	26.077	–97.2271
Praticolella griseola	9.5 km N of Puente Arroyo Hondo, (N of Veracruz), VC, MEX	ANSP A22080	20.0883	–96.9106
Praticolella griseola	9 km N of Papantla, VC, MEX	ANSP A22082	20.46389	–97.34111
Praticolella griseola	Tula, NL, MEX	ANSP A22081	23	–99.7167
Praticolella griseola	San Rafael, VC, MEX	ANSP A22075, ANSP 426022	20.2	–96.85
Praticolella griseola	Veracruz, VC, MEX	ANSP A22078, ANSP 426029	19.2147	–96.16028
Praticolella griseola	La Mancha, VC, MEX	ANSP A22073, ANSP 426019	19.6061	–96.39889
Praticolella griseola	1.5 mi S of Jiménez, TMP, MEX	ANSP 426028	24.2167	–98.4667
Praticolella griseola	1 km E Howey Height, Lake Co. Fl	ANSP A22084	28.667676	–81.746159
Praticolella mexicana	Diente, ~5 km S of Monterrey, NL, MEX	ANSP A22072 ANSP 426018	25.47728	–100.28673
Praticolella mexicana	Anahuac, NL, MEX	ANSP A22086	27.2519	–100.125
Praticolella mexicana	Puente San Rodrigo, COAH, MEX	ANSP A22089	28.6668	–100.9127
Praticolella mexicana	~10 km W of Monterrey, NL, MEX	ANSP A22077, ANSP 426025	25.67861	–100.4481
Praticolella mexicana	3 km N Agua Buena, Rio Tamasopo, SLP, MEX	ANSP A22087	21.9419	–99.395
Praticolella mexicana	Key Largo FL	ANSP A22091	25.17202	–80.3666
Praticolella mexicana	2 km N Agua Buena, SLP, MEX	ANSP A22088	21.96426	–99.38899
Praticolella mexicana	Hidalgo, Hidalgo Co. TX	ANSP 426020	26.1	–98.263
Praticolella mexicana	15 km SW of Linares, where road to Caja Pinta runs along stream, NL, MEX	ANSP A22101, ANSP 426032 (Paratypes)	24.7573	–99.6581
Praticolella mexicana	~5 km E Ciudad Victoria, TMP, MEX	ANSP A22085	23.7333	–99.1333
Praticolella mexicana	20 km N Mante, TMP, MEX	ANSP 426027	22.8833	–99.0167
Praticolella mexicana - int	USDA - JFK international airport interception from Dominican Republic	ANSP A22094	40.6501	–73.9496
Praticolella mexicana - int	USDA - Progresso from Mexico	ANSP A22093	26.0923	–97.9572
Praticolella mexicana	Hell, Grand Cayman	USDA-APHIS Collection	19.381774	–81.415936
Praticolella mexicana	Staniard Creek, Andros Island, Bahamas	ANSP A22090	24.844126	–77.892870
Morphometrics localities				
P. mexicana	15 km SW of Linares. In grass along fence at S end of park next basketball court, next to small stream. where Mx 58 to Caja Pinta runs along stream, NL, MEX	ANSP 426031 (Holotype), ANSP 426032, ANSP A22101 (Paratypes)	24.7573	–99.6581
	Canoas, SLP In park in town on road through town by stream.	ANSP 426026	21.94405	21.94405
P. berlandieriana	Milam County near Brazos River, 4.7 mi NE of Gause, USA, Texas	FMNH 259146	30.8289	–96.6706
	3.3 mi N New Braunfels, Comal Co.	ANSP 426023	29.7635	–98.1547
	20 M from Guadalupe River across from Guadalupe Canoeing 9 km N New Braunfels, Comal Co. TX	ANSP 426024 ANSP A22076	29.7739	–98.1601
	"Habite le Mexique, dans la province de Texas."	MHNG 37027		

(*Continued*)

Table 1. (Continued)

Species	Locality	Museum Number	Latitude	Longitude
"Praticolella griseola" Cameron Co	Cameron County, Port Brownsville, TX, USA	FMNH 259156	25.949904	–97.402715
	0.3 mi E Point Isabella high school, Port Isabel, Cameron Co. TX	ANSP 426021 ANSP A22074	26.077	–97.2271
Praticolella griseola	Nicaragua	FMNH 33486	12.865416	–85.207229

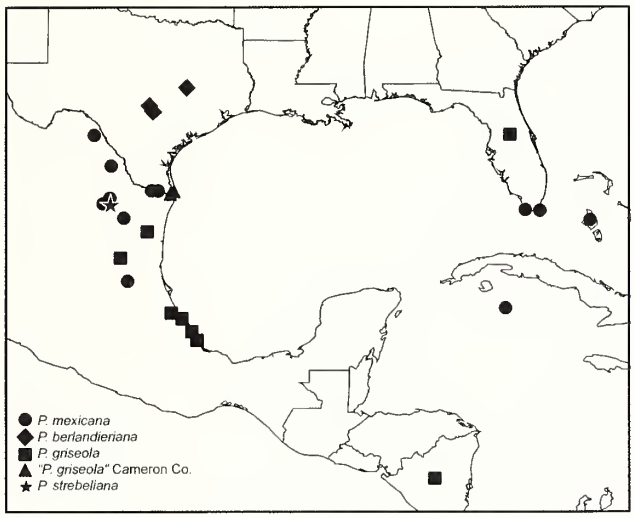


Figure 1. Map of specimens used for DNA analysis and additional localities of specimens used for morphometric analysis.

Individual sequences are available on Genbank, 16S: DQ085935-DQ086020, COI: DQ086021-DQ086095. Outgroups were included from other members of the Polygyrini (Emberton, 1995), specifically, *Polygyra cereolus* (Mühlfeld, 1816) and *Polygyra septemvolva* (Say, 1818).

Molecular Data Analysis: Total genomic DNA was extracted from several milligrams of tissue digested with CTAB lysis buffer and purified through standard phenol-chloroform procedures (Palumbi et al., 1991). Degenerate primers (5′-YRMCTGTTTAWCAAAAACAK-3′ and 5′-CCGGTCTGAATCCAGATCABGT-3′) were designed from the Palumbi et al. (1991) primer pair and Genbank sequences that amplified a ~450 bp fragment of the mitochondrial 16S gene. The Folmer et al. (1994) primers were used to amplify a ~600 bp fragment of the mitochondrial cytochrome oxidase c subunit I gene (COI) gene. Fragments were amplified by PCR, purified through gel extraction, and sequenced using BigDye 3.1 chemistry on an ABI 3100 automatic genetic analyzer. Specific protocols for amplification and sequencing can be found in Percz et al. (2005).

Sequences were assembled in Sequencher™ 4.0.5 (Gene Codes Corporation, Ann Arbor, MI) or Geneious Pro 3.5.6 (Drummond et al., 2006) and aligned in Muscle (Edgar, 2004). Garli 0.951 (Zwickl, 2006) was used to carry out maximum likelihood (ML) estimation of relationships. The ML analysis was carried out using Garli's default settings, as was an additional 100 replicate bootstrap analysis.

Shell Morphometric Analysis: In total, 237 specimens representing the following five species were examined: *P. berlandieriana* (46 specimens), *"P. griseola"* Cameron County (32), *P. griseola* (68), *Praticolella* new species (described below) (85), *P. strebeliana* (5) (Specimens used for DNA are listed in Table 1). We had difficulty in identifying to species specimens without living tissue for sequencing (shell-only specimens). Therefore, only a limited number of individuals from museum collections could be used for morphometric analysis, in addition to the individuals for which we gathered sequence data for morphometric analysis; this number mostly includes additional individuals or shell-only collections from the same locality as individuals with sequenced DNA. Color images were captured with a tripod-mounted, Canon PowerShot S3IS digital camera. Twenty-five landmarks (Figure 2) were digitized using tpsDig 1.31 (Rohlf, 2001).

Geometric morphometrics analyses were carried out using the Integrated Morphometrics Package, this includes the programs CoordGen, PCAGen, CVAGen, TwoGroup, and Regress 6 listed below (IMP software suite; Sheets, 2003) were used to examine shape variation through principal component analysis (PCA) and canonical variance analysis (CVA). PCA is a technique for simplifying descriptions of variation among individuals, while CVA simplifies descriptions of differences between pre-determined groups (Zelditch et al., 2004). In traditional morphometric analysis, PCA generally suffers from the overwhelming influence of size across the newly generated axes. However, geometric morphometric analysis eliminates size as a factor, yielding examinations of shape solely. In PCA, no *a priori* assumptions are needed to group individuals. In contrast, CVA determines the set of axes that best discriminates between groups; therefore an *a priori* assumption of group membership is necessary. For CVA analysis,

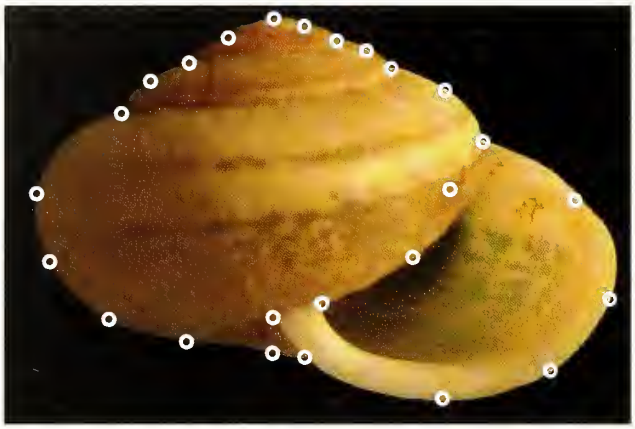


Figure 2. *Praticolella mexicana* individual (#436) from 15 km SW of Linares, Nuevo León, (ANSP 426031) Mexico showing landmarks used in the morphometric analysis. This individual used in both DNA and morphometric analyses.

individuals were grouped according to the clades identified by the molecular analysis.

Landmark coordinates were imported into CoordGen6f and converted to Procrustes distances using least squares Procrustes superimposition methods. A MANOVA carried out in SYSTAT 8.0 was used to examine differences in shape between species. Pairwise comparisons between all populations were performed in TwoGroup6c with Bonferroni correction to determine if there were significant shape differences. A PCA was performed with PCAGen6g on the data with *a posteriori* groups assigned by locality. A CVA was also performed using CVAGen6h with groups defined by the clades from the DNA analysis. The difference in shape between each species was examined directly using Regress6.

Abbreviations and Text Conventions: MHNG = Museum d'Histoire Naturelle, Geneva; FMNH = Field Museum of Natural History; ANSP = Academy of Natural Sciences of Philadelphia (ANSP numbers beginning with "A" represent lots preserved in alcohol); USDA = United States Department of Agriculture; GM = geometric morphometric analysis; PCA = principal component analysis; MANOVA= multivariate analysis of variance. Latitude and Longitude presented in decimal degrees.

RESULTS

Molecular Phylogeny: Maximum likelihood analysis of 417 bp of 16S and 493 bp of COI yielded a single tree (Figure 3). *Praticolella* new species (to be described below) comprised a well-supported monophyletic clade. Many individuals included in this clade were initially identified as *P. berlandieriana* due to their geographic location in northeastern Mexico. Some individuals in this clade were from invasive populations (Bahamas and Florida) or United States Department of Agriculture (USDA) interceptions and were initially identified as *P. griseola*, which is well known as invasive. The DNA tree also shows monophyletic lineages from both near Victoria, Tamaulipas, and near Mante, Tamaulipas. These are herein considered part of *Praticolella* new species , but further work is needed to examine population level versus species level differences among these lineages.

Individuals conforming to the morphology of *P. griseola*, including topotypic material, form a clade (100% bootstrap support; labeled *P. griseola* on Figure 3) that has deep subdivisions between different populations in the mitochondrial DNA and includes an individual from an invasive population in Lake County, Florida. The *P. griseola* clade is resolved as sister (75% bootstrap support) to a monophyletic group of individuals from Soto la Marina, Tamaulipas. Individuals from a small, morphologically unique, disjunct population of *P. griseola* were sampled in this study and are called here: "*P. griseola*" Cameron Co. (Pilsbry, 1940; Rehder, 1966). This population formed a distinct clade separate from *P. griseola*, but due to poor support in this portion of the tree, relationships remain uncertain.

Individuals from as close to the type locality of *P. berlandieriana* as could be determined (details below, within 30 km) form a clade sister to other Texas *Praticolella* species (84% bootstrap), including individuals of *P. trimatris* Hubricht, 1983, *P. pachyloma* (Menke in Pfeiffer, 1847) and *P. taeniata* Pilsbry, 1940.

Shell Morphometric Analysis: Differences in shell shape in *Praticolella* were assessed using GM (Figure 3). Shell variation is traditionally quantified through straight-line shell measurements and ratios and used to distinguish between individuals and populations at the species level (e.g., Heller et al., 2005; Tanaka and Maia, 2006). Recently, GM has been employed in examinations of snail shells, both to provide direct size-free analyses of shell shape and to answer broader evolutionary questions (Pfenninger and Magnin, 2001; Conde-Padin et al., 2007; Hayes et al., 2007).

The first PCA axis (PC1) explained 31.5% of the variation, the second (PC2) explained 15.3%, and the third (PC3), 13.1%. A MANOVA on the PCA scores found a significant difference among groups (Hotelling-Lawley Trace=2.012, F-Statistic=30.669, df=15, 686, $p<0.000$). Pair-wise comparisons of all species assessed by Goodall's F test showed that snails from each species had significantly different ($p<0.01$) shapes.

Each species was compared pairwise using TwoGroup to carry out Goodall's F-test. Pairwise comparisons were followed by a Bonferroni correction. This analysis found that each of the species' means are significantly different ($p<0.001$ in all cases). The lectotypes (ANSP 411457 and 77128) of *Praticolella strebeliana* are distinct on the first three PC axes (Figure 4) with the highest difference in mean value from the other species (Distance in mean value from *P. griseola*=0.0967; *P. berlandieriana*=0.0916;

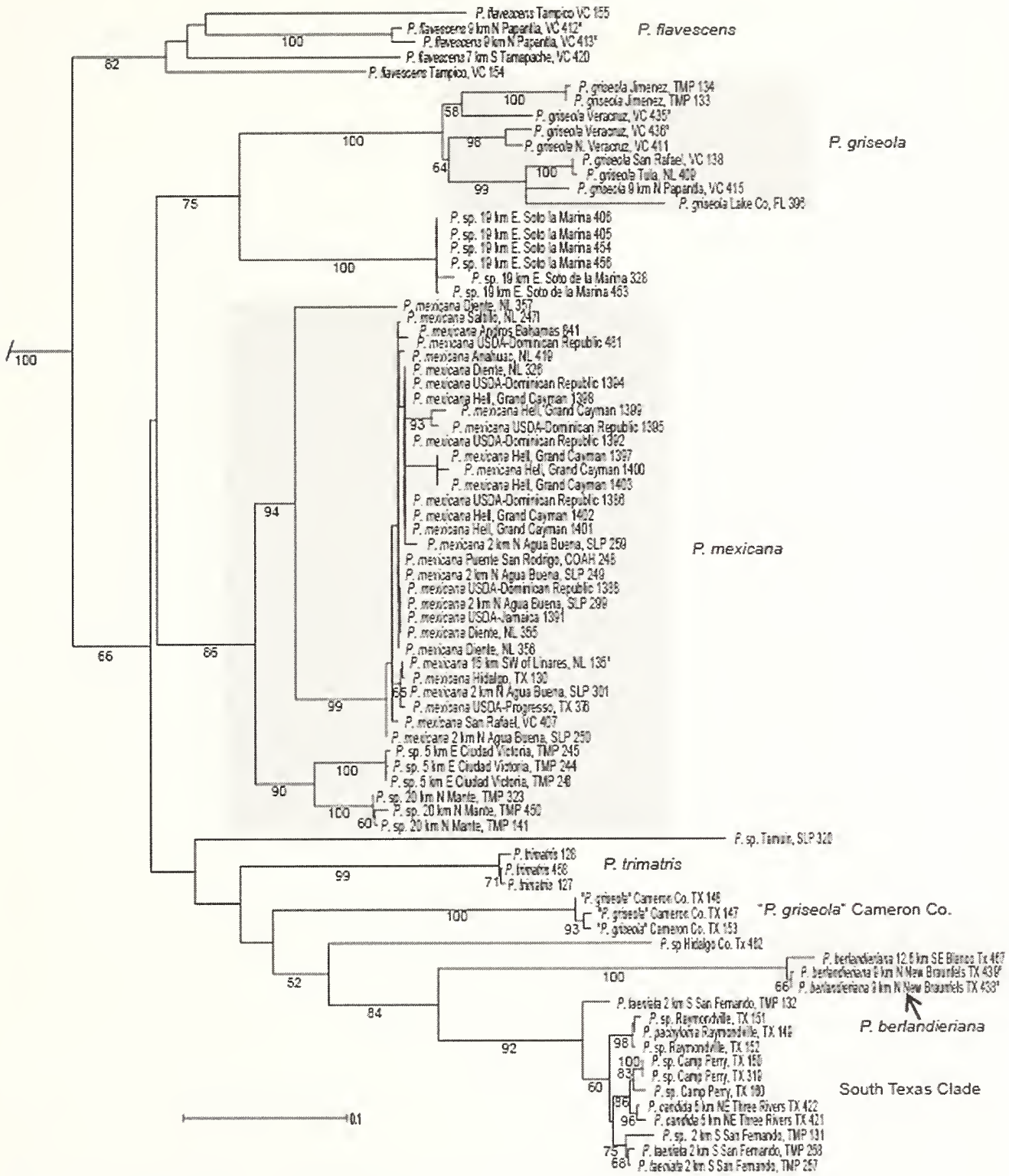


Figure 3. Molecular phylogeny of *Praticolella*. Maximum likelihood phylogram based on 16S and COI mitochondrial DNA. The species discussed in this paper are marked by grey boxes. Numbers on branches are ML bootstrap values. Outgroups not shown.

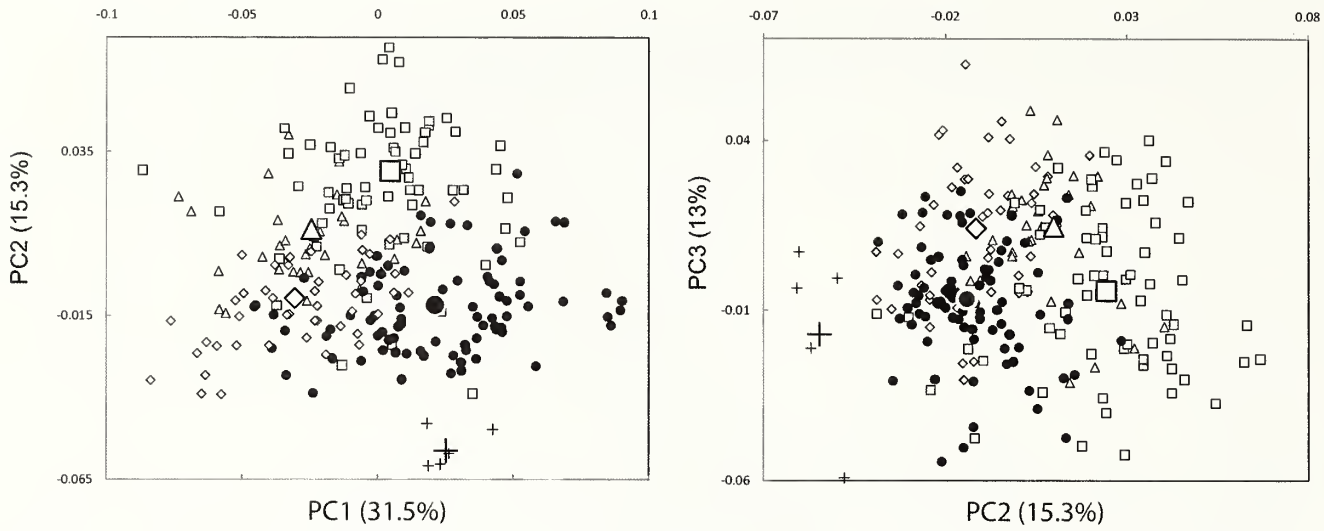


Figure 4. Principal component axes 1, 2, and 3. Percentages indicate the percent of the variance explained by each axis. Large symbols represent group means: *Praticolella mexicana* (•); *P. berlandieriana* (◊); *P. griseola* (□); "*P. griseola*" Cameron Co (Δ) *P. strebeliana* (+).

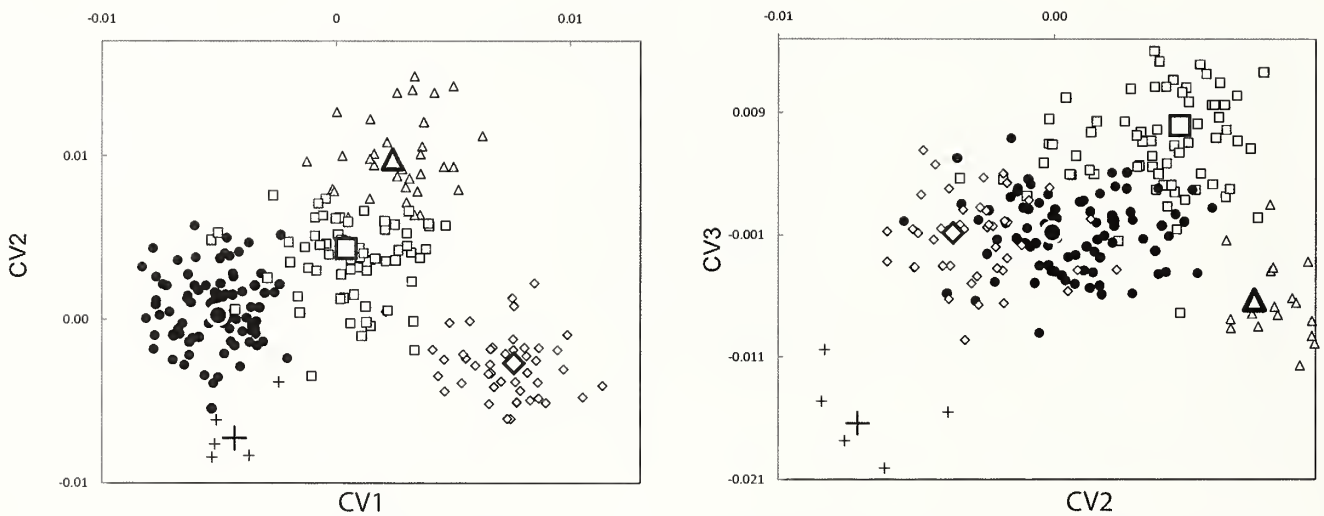


Figure 5. Canonical axes 1, 2, and 3. Discriminant scores calculated to maximally separate the five species. Left: the first and second canonical axes. Right: the second and third canonical axes. Large symbols represent group centroid. *Praticolella mexicana* (•); *P. berlandieriana* (◊); *P. griseola* (□); "*P. griseola*" Cameron Co (Δ) *P. strebeliana* (+).

Praticolella new species=0.0723). Although the species are significantly different, visual examination of Figure 4 shows there is a great deal of overlap in the shape variation present in each species. *Praticolella* new species is the most distinct in shape (Distance in mean value from *P. griseola*=0.0448; *P. berlandieriana*=0.0590; *P. strebeliana*=0.0723), but *Praticolella* new species, *P. griseola* and *P. berlandieriana* also have a great deal of overlap in shape (Figure 4; Distance in mean value=0.0518). CVA of each population yielded four distinct axes ($p < 0.05$) where all centroids were significantly different from each other (Figure 5). The resulting plot of CV 1 and CV 2 shows very little overlap among species, although a few individuals of *P. griseola* (three of 64) overlap into the new species' shape space. One individual of *Praticolella* new species grouped with *P. griseola*. The plot of CV2 and CV 3 widely separate *P. strebeliana* and *P. griseola* from the other species. Finally, "*P. griseola*" Cameron Co. is significantly different from the other species and distinct from *P. griseola* and *Praticolella* new species in all analyses. Figure 6 shows how shell shape differs from *Praticolella* new

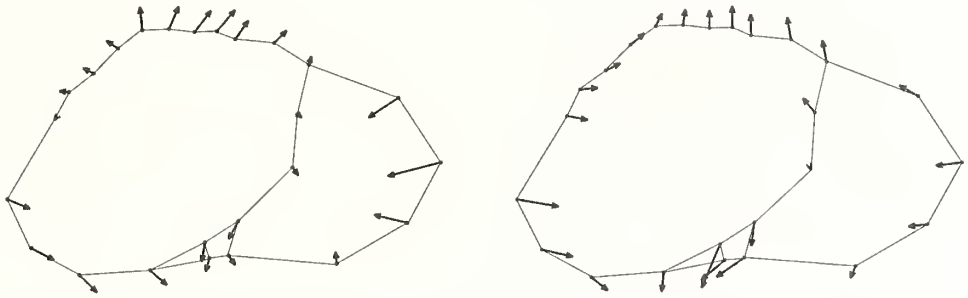


Figure 6. Change in shell shape between species. Left: Shape change to *P. berlandieriana* from *P. mexicana*. Right: shape change to *P. griseola* from *P. mexicana*. Shape change is exaggerated 3X by vector arrows to ease interpretation.

species to *P. berlandieriana* and (left) and from *Praticolella* new species to *P. griseola* (right).

SYSTEMATICS

Family Polygyridae Pilsbry, 1930

Genus ***Praticolella* von Martens, 1892**

Dorcasia Binney, 1878: 356.
Praticola Strebel and Pfeiffer, 1880: 38.
Praticolella von Martens, 1892: 138.

Type Species: *Praticolella ampla* (Pfeiffer, 1866), by original designation.

Diagnosis: Shell small, globose to slightly depressed with a conic spire of 4.5 to 5.75 whorls. Aperture either slightly or greatly reflected and without denticles. Narrowly umbilicate (Pilsbry, 1940). Penial divertieulum long and at least twice the volume of the penis (Emberton, 1995). Bifurcate or trifurcate penial retractor muscle (Emberton, 1995).

Distribution: United States: Florida, Georgia, Alabama, Mississippi, Louisiana, North Carolina, Texas, Mexico south to Panama, Caribbean islands.

***Praticolella mexicana* new species**
Figures (7–13)

Praticolella berlandieriana (Moricand, 1833): Fischer and Crosse, 1872: 256-257; Vanatta, 1915: 194, fig. 1 (genitalia); Pilsbry, 1940: 695, fig. 427a; Rehder, 1966: 290-291, fig. 20; Correa-Sandoval, 1993: 685; Correa-Sandoval, 1996: 137; Correa-Sandoval, 1999: 15; Correa-Sandoval, 2000: 493; Correa-Sandoval and Castro, 2002: 238.
Praticolella griseola Pfeiffer, 1841: Robinson, 1999: 415.

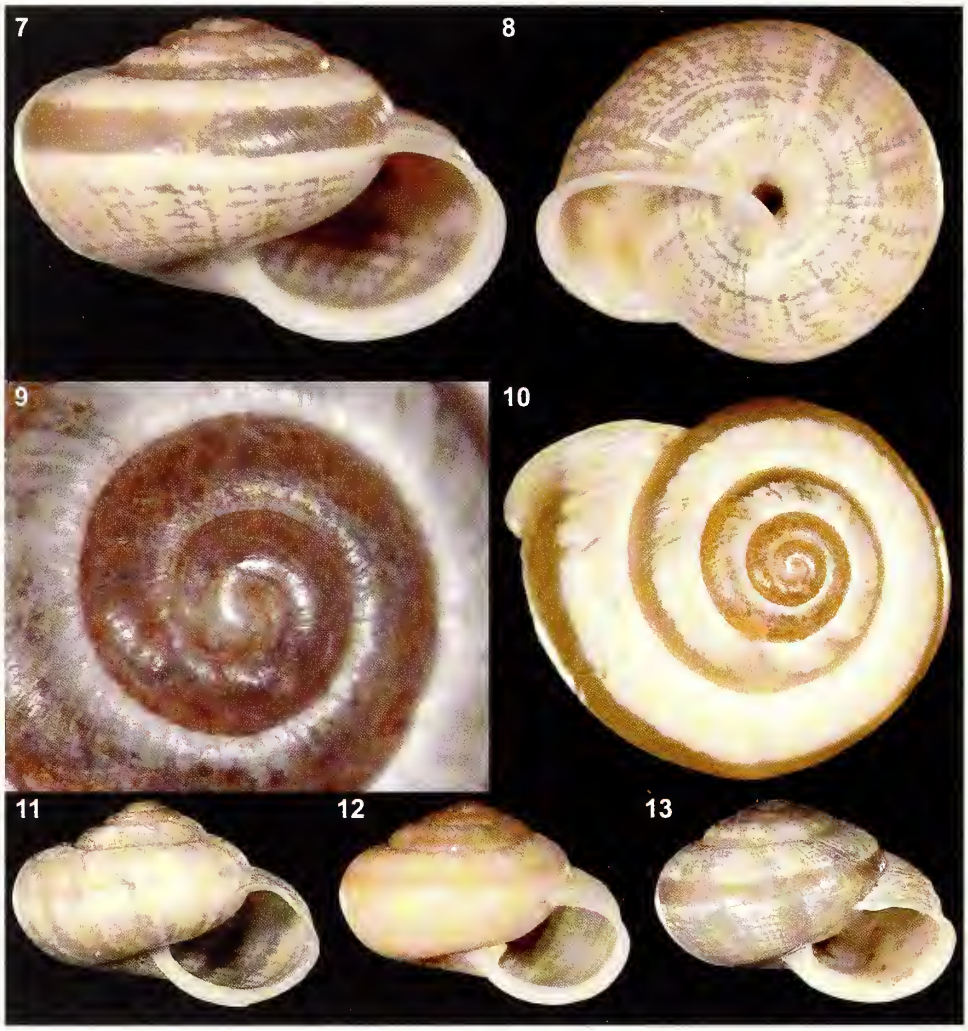
Description: Shell umbilicate, globose to somewhat depressed-globose. Lip thin, refleeted to slightly cover umbilicus. Banding extremely variable, ranging from unbanded brown shell, unbanded white shell, to having nine eomplete and incomplete bands, radiating lines of white pigment, and streaks of white pigment on body whorl. Umbilical whorls with fine growth lines but no spiral striae and usually brown/gray eolored with no white pigment, shiny. Average shell height=7.57, width=10.87, umbilicus width=0.69 mm, 5–5.6 whorls (Table 2).

Type Material: Holotype ANSP 426031, 27 May 1992, Ned E. Strenth (Figures 7–10). Paratypes ANSP 426032 and alcohol-preserved speeimens ANSP A22101. Other material examined: Hidalgo, Hidalgo Co. TX, 21 Sept. 1991, Ned E. Strenth (Figure 11), ANSP 426020; College of the Bahamas Research Station, Staniard Creek, Andros Island, Bahamas, 20 May 2005, K. E. Perez, ANSP A22090 (Figure 12); Canoas, San Luis Potosí, Mexico, 23 July 2002, K.E. Perez, J.B. Pollock, ANSP 426026 (Figure 13).

Type Locality: 15 km SW of Linares, Nuevo León, Mexico, in grass next to small stream where MX 58 to Caja Pinta runs along stream, 24.757331 N, –99.658111 W.

Distribution and Habitat: Widely distributed in northeastern Mexieo and south Texas on the eastern side of the Sierra Madre Oriental. There may be native populations in south Texas, though the collections examined were all from disturbed habitat or greenhouses. United States Department of Agriculture (USDA) often intercepts this species at the Texas/Mexico border. Introduced populations were found in Florida, Bahamas, Grand Cayman Island, Dominiean Republie, Haiti, and Cuba. Several USDA interceptions were from Jamaica and Turkey. The native range of this species is most likely northeastern Mexico, north and east of the Sierra Madre Oriental. First, the basal lineages in this clade are all found in this region of Mexieo. Second, collections from this region of Mexico predate the collection of this species in the Caribbean or Florida. This species was first reported as introductions collected in disturbed habitats of Florida in the early part of the 1900's.

The preferred diet of this speeies is unknown; however, it has been found on ornamental (greenhouse) plants and



Figures 7–13. Shells of *Praticolella mexicana* new species. **7–10.** Holotype, SW of Linares, Nuevo León, Mexieo, 27 May 1992, Ned E. Strenth, ANSP 426031; side, top, and basal views of the shell and embryonie whorls, w=9.58 mm, h=6.59 mm, 5.25 whorls. **11.** ANSP 426020, Hidalgo, Hidalgo Co. Texas, w=10.59, h=7.46, 5.25 whorls, 21 Sept. 1991, Ned E. Strenth eoll. **12.** ANSP A22090, College of the Bahamas Research Station, Staniard Creek, Andros Island, Bahamas, w=10.57, h=7.63, 5.25 whorls, 20 May 2005, K.E. Perez eoll. **13.** ANSP 426026, Canoas, San Luis Potosí, Mexieo, w=9.79 mm, h=7.18 mm, 5.25 whorls, 23 July 2002, K.E. Perez, J.B. Pollock colls.

Table 2. Shell measurements for the three speeies of *Praticolella*. Only adult shells with a full lip were measured: *P. berlandieriana* (n=24), *P. griseola* (n=36), *P. mexicana* (n=37). Values present, from top, range, mean and standard deviation. Abbreviations: h: shell height; w: shell width; aph: aperture height; apw: aperture width; umb: umbilicus width; # of whorls – number of whorls.

Speeies	h (mm)	w (mm)	aph (mm)	apw (mm)	umb (mm)	# of whorls
P. mexicana	6.3–9.19	9.38–12.27	4–6.77	4.85–6.92	0.4–1.08	5–5.6
	7.57±0.61	10.87±0.78	5.28±0.51	5.97±0.60	0.69±0.15	5.30±0.17
P. griseola	8.32–11.29	5.8–7.92	4.4–6.7	4.16–5.75	0.38–1.03	4.75–5.5
	9.65±0.78	6.91±0.51	5.34±0.47	4.88±0.39	0.71±0.16	5.12±0.16
P. berlandieriana	9.92–11.73	7.34–8.75	4.5–6.14	4.65–5.77	0.64–1.18	5–5.5
	10.49±0.49	8.16±0.40	5.52±0.42	5.19±0.29	0.85±0.13	5.35±0.22

is common in sugarcane, citrus, mango, banana, aloe, and papaya plantations (USDA interception records). The USDA has intercepted this species on shipments of mangos, papayas, ornamental plants, and furniture. These snails possess many of the typieal characteristics of invasive snail speeies, such as living at high population densities in shrubs, tall grass, and under trash. This speeies is often found climbing walls and grass.

Etymology: Named in reference to the native distribution of this speeies in Mexieo.

Taxonomic Remarks: *Praticolella mexicana* is similar to *P. griseola*, but differs in being larger, having a more robust, depressed shell with white pigmentation, a flattened wide body whorl, and a more oval-shaped aperture. Figure 6 (right) illustrates the differenee in shape between *P. mexicana* and *P. griseola*. The body whorl of *Praticolella griseola* (Figure 14) is more rounded with a rounded aperture. The insertion of the peristome is mueh eloser to vertieal in *P. griseola* and horizontal in *P. mexicana*. *Praticolella berlandieriana* is distinguished from *P. mexicana* by having a taller, much thicker, heavier shell and widely expanded lip (Figure 6 left and 20).

Praticolella strebeliana was ineluded in this study as it was deseribed from Diente Mine near Monterrey, Nuevo León Mexieo (Pilsbry, 1899) within the range of collections of *P. mexicana*. This species was described as eompletely brown with no bands; however, because oeeasionally *P. mexicana* individuals have no bands (populations from Hidalgo, Texas are all bandless with a brown base eolor), I thought it necessary to consider *P. strebeliana* as potentially having priority before naming this new taxon (*P. mexicana*). Therefore, to test whether *P. strebeliana* was an appropriate name, *Praticolella* specimens from Diente, the type loeality of *P. strebeliana*, were colleeted for both DNA and morphometrie analyses. Several colleeting attempts at the type locality yielded no unbanded shells fitting the description of *P. strebeliana*. All individuals sequenced from this loeality are within the *P. mexicana* clade. Therefore, I have no DNA evidenee to distinguish *P. strebeliana*. However, morphometrie analysis of the type speeimens (ANSP 77128 and 411457) of *P. strebeliana* showed that they were very distinet from *P. uexicana*, *P. berlandieriana*, and *P. griseola* (Figures 4 and 5). *Praticolella strebeliana* has a frosted, corneous shell that is more globose than *P. mexicana*, as well as a downward tilted lip and greater degree of eontraetion behind the lip. Based on the differences in shell morphology and morphometric analysis I am considering *P. strebeliana* distinct from *P. mexicana*. In texture and eoloration of the shell, *P. strebeliana* is more similar to *P. flavescens* than the other Texas or Mexiean taxa.

Praticolella griseola (Pfeiffer, 1841)

Helix cicercula Férrusac in collection = *griseola* according to Pfeiffer 1848, 1: 337.
Bradybaena pisum Beck, 1837: 18 (*nomen nudum.*)
Helix griseola Pfeiffer, 1841: 41; Pfeiffer, 1848: 337.
Helix albocincta Binney, 1851: 109, 128.
Helix albo-zonata Binney, 1857: pl. 49, fig. 2.
Helix albolineata Gould in Binney, 1857: 34.
Helix splendidula Anton, 1839: 36. (*nomen nudum*).
Dorcasia griseola Pfeiffer, 1841; Binney, 1878: 348, fig. 231 (jaw), pl. vii, fig. v (teeth).
Helix berlandieriana var. *griseola* Pfeiffer, 1841; von Martens, 1892: 140, pl. 7, figs. 15–17.
Helix (*Praticola*) *griseola* (Pilsbry, 1891): 313.
Praticolella griseola Pilsbry, 1940: 690–692, fig. 425.

Description: *Praticolella* with a robust, umbilicate, depressed-globose shell. Number of pigmented bands on body whorl ranges from 1 to 8 with most shells having 2 or 3. Most individuals possess a complete cinnamon eolored mid-body whorl band. Aperture lunate to round with a thin reflexed lip. Shell obliquely striate. Average shell height=9.65, width=6.91, umbilieus width=0.71 mm, 4.75–5.5 whorls (Table 2).

Type Material: Syntypes, 6 individuals, Mexieo. Natural History Museum of London 20110179. Figures 14–19.

Distribution and Habitat: Pfeiffer (1841) gave the type locality of *P. griseola* as Veraeruz. This speeies is native to Veraeruz and southern Tamaulipas and has also been introduced to South Florida and New Orleans, Louisiana. Due to restrietion of populations in the Yueatán and Guatemala to disturbed areas, it is considered invasive there as well (Harry, 1950). However, native populations in Guatemala have not been ruled out by this data. The complete range of this species will need further work to be fully circumseribed. Specimens labeled *P. griseola* in museum eolleetions are often *P. mexicana*.

Taxonomic Remarks: *Praticolella griseola* was described by Pfeiffer (1841) in a short paragraph without illustration. The specimens are attributed to Hegewisch, referring to the physician and botanical collector Dr. Ernst Friedrieh Adoph Hegewisch, who lived in Oaxaca, Mexico, around 1836–1840 (Pritzel, 1864). Pfeiffer's primary colleetion (collection 532) was lost with the destruetion of the Stettin Museum (Danee, 1986). However, some Pfeiffer material resides in the Natural History Museum in London (NHMUK) including a lot of 6 speeimens labeled "*H. griseola* Mexico Pfr" in Pfeiffer's handwriting (handwriting identified by Jonathan Ablett, Curator of Non-Marine Mollusea and Cephalopoda, NMHUK, pers. comm.). These specimens were also labeled "M.C." indieating they came from the Hugh Cuming colleetion. While it is not possible to conelude that these specimens were from the original type series, Pfeiffer's handwriting on the label indicates they are probable syntypes.

In the phylogenetie tree (Figure 3), topotypic specimens conforming to the original description of *P. griseola* formed a monophyletic lineage with individuals from an introdueed population in Florida as well as speeimens from the coastal plain of Veracruz and north into Tamaulipas.

Praticolella griseola has been the subject of mueh taxonomie eontention. Von Martens (1890–1901) and Singley (1893) stated that *H. griseola* and *H.* (*Praticolella*) *berlandieriana* are connected by many intermediate forms and eannot be maintained as distinct speeies.

Figures 14–19. Shells of *Praticolella griseola*. **14–19.** Syntypes, Mexico, Pfeiffer material, H. Cuming Collection MNHUK 20110179. **14–17.** Side, top, and basal views of the shell and embryonic whorls. Scale bar = 1 mm (Figure 14). **18.** Side view of additional shell from same lot. **19.** Side view of additional shell from same lot.

However, Pilsbry (1940) found no connecting links between *P. griseola* and *P. berlandieriana* and further proposed that they formed an ecological pair with *P. griseola* living in warmer more humid regions, and *P. berlandieriana* living in cooler, semiarid country. However, Cheatum and Fullington (1971) stated, without presenting evidence, that, due to interbreeding, in a large assortment of shells representing all species (meaning all species present in south Texas) from the same geographic area it is difficult to determine where one species ends and another begins.

Praticolella griseola has been suggested to be made up of a number of well-characterized "races" living in a variety of habitats and climates (Rehder, 1966; Neek, 1977). Rehder's (1966) "races" of *P. griseola*, included the populations around Veracruz, Mexico and a second race comprised of a small, unique, disjunct population in Cameron County in south Texas. Individuals from this "race" were sampled in this study and are referenced herein as "*P. griseola*" Cameron Co. (Pilsbry, 1940; Rehder, 1966). These snails have a thinner lip and a dark-colored basal whorl. Taxonomic placement of this population is outside of the sampling and scope of this study, but the mitochondrial DNA results indicate that it is distinct from *P. griseola* and from other nearby *Praticolella* species and remains to be described.

Praticolella griseola has deep subdivisions between different populations in the mitochondrial DNA analysis. The individuals from Jiménez in particular are distinctive in morphology as well in that they have a slightly heavier lip and more solid shell. They also have more regular spiral striae on the embryonic whorl than typical *P. griseola*.

Praticolella berlandieriana (Moricand, 1833)

Helix (Helicogena) berlandieriana Moricand, 1833: 537, pl. 1, fig. 1.
Helix berlandieriana Moricand, 1833: Leidy in Binney, 1851: 255, pl. 8, fig. xi.
Doreasia berlandieriana (Moricand, 1833): Binney, 1878: 347.
Praticolella berlandieriana (Moricand, 1833): Pilsbry & Ferriss, 1906: 125–126, figs. 1 and 2; Pilsbry, 1940: 694–697, fig 427b (shell); Webb, 1967: 133–136, figs. 12–17.

Description: Shell solid, narrowly umbilicate, globose-depressed with a low conic spire. Color white to gray to light buff, frequently with a gray band above the periphery; other bands or colored streaks common. Embryonic whorls glossy, sometimes gray to light brown, sometimes with fine spiral lines; later whorls weakly striate. Body whorl rounded at the periphery, somewhat contracted behind the lip. Lip white, widely expanded, strongly thickened within (Figures 20–23). Average shell height=10.49, width=8.16, umbilicus width=0.85 mm, 5–5.5 whorls (Table 2).

Type Material: Syntypes MHNG 37027, "Habite le Mexique, dans la province de Texas" (Moricand, 1833)

Distribution and Habitat: Edwards Plateau biotic province (Blair, 1950), central Texas, extending north to Arkansas. In mesquite or grassy areas, often found under trash and on roadsides.

Taxonomic Remarks: *Praticolella berlandieriana* was described by Moricand (1833) referring to specimens with the locality noted as "Texas" collected by Jean Louis Berlandier, a botanist from Geneva who collected botanical specimens in Mexico. Berlandier collected intensively in Bexar and Comal counties as well as along the road to Gonzales, Texas in the spring of 1828 (Geiser, 1948).While it is not possible to know exactly where within this region Berlandier collected these shells, I am treating specimens collected for DNA analysis from Texas, North of the Balcones Escarpment, NE of the San Antonio area (New Braunfels and Blanco River collections) as the best possible representatives of this species. This highway route follows the historical road

Figures 20–23. Shell of *Praticolella berlandieriana*, ANSP 426024, 9 km N of New Braunfels, along the Guadalupe River, Comal Co. TX; side, top, and basal views of the shell and embryonic whorls. w=10.06, h=8.28, 5.5 whorls, 1 July 2004, K. E. Perez coll.

between San Antonio and Gonzales. DNA sequence analysis resolves these individuals of *P. berlandieriana* as a separate unique lineage; other individuals from Mexico that have been treated as nominal *P. berlandieriana* have been herein assigned to other species in the genus.

Von Martens (1890–1901) treated *P. berlandieriana* as part of the Mexican fauna and identified its range as Texas and much of northern Mexico. He also considered this species to be synonymous with *P. griseola* as reflected in his extensive synonymy. Rehder (1966) attempted to distinguish *P. griseola* from *P. berlandieriana* and restricted *P. berlandieriana*'s range to central Texas through southern Tamaulipas, Mexico. Hubricht (1983) considered *P. berlandieriana* to have specific rank; however, he considered this species to be of ancient hybrid origin derived from a combination of lineages of *P. pachyloma* and *P. candida*. Mitochondrial DNA does not support this conclusion (Figure 3).

Praticolella berlandieriana has been considered to have a large range, from central Texas to central Mexico (Pilsbry, 1940; Rehder, 1966; Cheatum and Fullington, 1971). This species was then considered restricted to central Texas by Neck (1977) and Hubricht (1983); however, the name has continued to be applied to Mexican species with individuals identified as *P. berlandieriana* reported by Correa-Sandoval (1993; 1999) from Nuevo León, Tamaulipas, and San Luis Potosí. However, the lack of any individuals further south than central Texas forming a clade with *P. berlandieriana* indicates that these Mexican records most likely represent *P. mexicana* new species or other undescribed Mexican *Praticolella*. All the *Praticolella* in south Texas fall into other clades (Figure 3: south Texas Clade, "*P. griseola*" Cameron County, or *P. trimatris*) Therefore, it appears that the distribution of *P. berlandieriana* should be restricted to central, east, and north Texas.

The internal anatomy of an individual of *P. berlandieriana* from Comal County, Texas, near the type locality as described in this paper, was figured in Webb (1967). *Praticolella berlandieriana* is also figured (Vanatta, 1915) from a specimen from Victoria, Tamaulipas but this illustration does not represent true *P. berlandieriana*.

DISCUSSION

This study is the first to use molecular data to examine and delineate species boundaries in the family Polygyridae. DNA sequences for 16S and COI were used to estimate relationships within the genus *Praticolella* with emphasis on *Praticolella griseola* and the species taxonomically confused with it. This analysis provides an evolutionary framework for further inter- and intraspecific studies within *Praticolella* as well as providing some baseline for management efforts of the several invasive *Praticolella* species.

Accurate identification and the continuing deposition of species in natural history collections are of primary importance for management of invasive species. Predictions of how newly introduced organisms may be capable of surviving or altering habitats or ecosystems cannot be made unless the species in question has been identified accurately. Attempts to control spread or population growth of these species is hindered because information on ecology of the introduced species within its native range cannot be gathered or used without a correct identification. In the opposite case, data gathered in the newly introduced environment cannot be used by workers in areas where they have been introduced previously.

Molecular analyses found several exclusive lineages of snails that had previously been treated/identified as *P. griseola*. There are multiple invasive lineages of *Praticolella* in the USA, and the majority of individuals encountered both in established populations and intercepted by USDA are *P. mexicana* from trade goods shipped from the Caribbean. This result indicates most of the propagule pressure for *Praticolella mexicana* invasion is actually via secondary invasion through the Caribbean, not coastal Mexico as previously thought. This species also appears to be starting to establish populations worldwide with the first USDA interceptions from Turkey in 2009 (USDA Interception Number: AP11TX062722570001).

Along with the discovery of multiple lineages of invasive species, this analysis also highlighted populations of *P. griseola* from south Texas, from a population disjunct from the rest of the species distribution by ~300 km. This population had long been regarded as a distinct "race" of *P. griseola* (Rehder, 1966; Neck, 1990); however, this study indicates this lineage is distinct and very limited in distribution.

In addition to the Cameron County, Texas lineage the molecular results of this study uncovered several very distinct lineages that cannot confidently have an available name applied. This includes the lineage sister to *P. griseola* from the Soto la Marina, Tamaulipas (TMP) area. Considered part of *P. mexicana* are two populations that form unique exclusive lineages, from near Ciudad Mante, TMP, and near Ciudad Victoria, TMP. Additional sampling will be required to determine the extent of the distribution of these lineages and their specific status. It is outside the scope of this paper and the available collection materials to circumscribe these species, but these molecular data suggests that there is much undescribed diversity within *Praticolella*.

The life-history characteristics of *Praticolella* lend this group of snails to an invasive life-style. They thrive in disturbed habitat, living at high population densities in shrubs, tall grass, and agricultural lands; consequently they frequently travel on citrus, vegetables, and ornamental plants. These species share a morphological type characterized by multiple color bands on the shell. These shell banding patterns have been proposed to be an adaptation for snails that climb up vegetation, thus providing camouflage from bird predators (Johnson, 1980), an alternative has been proposed that bands

provide thermal control by reducing radiative energy absorption (Burla and Gosteli, 1993). This characteristic is therefore likely to be convergent and not taxonomically useful, although it has been used extensively in previous taxonomy of *Praticolella*.

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Ten new bathyal and abyssal species of Scaphopoda from the Atlantic Ocean

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ABSTRACT

Ten new species of Scaphopoda (one of the Order Dentaliida and nine of the Order Gadilida) from bathyal and abyssal depths in the North Atlantic Ocean, Caribbean Sea, and northern Brazil are described. The material was collected during diverse expeditions carried out by European and American research institutions. The new species are named as, in the order Dentaliida: *Laevidentalium abyplaine* new species; and in the order Gadilida: *Pulsellum filiforme* new species, *Striopulsellum sandersi* new species, *Striopulsellum knorr* new species, *Striopulsellum atlantis* new species, *Cadulus unilobatus* new species, *Gadila celtica* new species, *Gadila cretea* new species, *Chistikovia atlantica* new species and *Siphonodentalium coronatum* new species. These findings confirm that the deep-water realm, even in regions historically considered as well known, are far from being adequately inventoried.

Additional keywords: Mollusca, deep-sea, new species, geographic distribution

INTRODUCTION

The scaphopod fauna recorded from the Atlantic Ocean includes some 132 species. Ninety of them are distributed over the western areas (including the Caribbean Sea to Sub-Antarctic waters) and 42 were reported from the eastern side (including the Mediterranean Sea and West Africa). Seven species are considered to have amphi-Atlantic distribution. For the northwestern Atlantic and Caribbean, the first comprehensive revision was published by Henderson (1920). Subsequent taxonomic arrangements and some new species descriptions did not substantially modify their number. In the northeastern Atlantic region, since early discoveries, the number of species remained notably stable. More than 85% of species (36) were described during the 19th Century. The most prolific authors at the time were Jeffreys (1877, 1883) who described nine species, M. Sars (1859, 1865) and Locard (1897), who described four. More recently, Nicklès (1955, 1979) described twelve new species from western Africa, but, for the northeastern region, it was not until 1979 that a new species, *Siphonodentalium laubieri*, was described from bathyal depths of the Norwegian Sea (Bouchet and Warén, 1979). Later, Scarabino (1986 a, b) described respectively two other abyssal species: *Wemersoniella turnerae* and *Annulipulsellum euzkadii* (both amphi-Atlantic, see Caetano et al., 2006). Those papers also include two other new species, described from the abyssal realm of the Argentinian Basin (from 5332–5781 m): *Wemersoniella duartei* and *Costentalina venae*. Detailed information on localities and type depositories of the species registered for this large region is given in Steiner and Kabat (2004).

During revision of bathyal and abyssal collections in localities of the Atlantic Ocean, a surprising number of new species (one belonging to Dentaliida and nine to Gadilida) were identified and are described here. Five of them were collected only in the North and central Atlantic basins, two have amphi-Atlantic distribution and three come from diverse localities of the western Atlantic such as the Puerto Rico Trench and northern Brazil basins. The Atlantic deep-sea records mentioned for *Chistikovia* Scarabino, 1995 and *Striopulsellum* Scarabino, 1995 genera given by Scarabino (1995: 323, 327) refers to the species here recorded. The finding of the ten new species here described confirm that the deep-water realm, even in regions historically considered as well known, are far from being adequately inventoried.

MATERIALS AND METHODS

The material was collected during oceanographic cruises carried on by European and North American institutions. The first group were mostly French and made in

the Gulf of Gascony: Biogas I–XII (1972–1981) and Incal (1973); off Portugal and Spain: Abyplaine (1982); North Atlantic: Noratlante (1969); off Azores: Biaçores (1971) and in the Vema Trench: Biovema (1977), all IFREMER/MNHN. Additional European materials came from expeditions of the R/V Ingolf (1895) (ZMUC) and R/V Princesse-Alice II (1911) (MOM). North American cruises, all WHOI, were carried out in the Puerto Rico Trench: R/V Knorr cruise 25 (1972), Blake Plateau and North American Basins: R/V Knorr cruise 35 (1973), R/V Chain, cruises 50 and 106 (1965, 1972); and the Pernambuco Trench: R/V Atlantis II cruise 31 (1967). The total represents 56 localities in depths from 1456 to 5875 m, 40 of which carried out below 4000 m depth.

For further information on the expeditions Abyplaine (1982); Biaçores (1971), Biogas I to XII (1972–1981), Biovema (1977), Incal (1973) and Noratlante (1969), see http://www.ifremer.fr/biocean/acces_fr/data_fr.htm; R/V Atlantis II; R/V Chain and R/V Knorr (WHOI) between 1967 and 1972, http://www.whoi.edu/; Ingolf, 1895 in: Results of the Danish Ingolf-Expedition, Copenhagen; R/V Princesse-Alice II (1911) Results of the scientific campaign of the Prince of Monaco, vol 89.

Radula: As stated in Scarabino and Scarabino (2010), the scaphopod radula is large enough to facilitate visualization of the different teeth of that convey taxonomic information. The radula is especially useful in taxa of the Order Gadilida, in which the small rachidian teeth are always covered by the laterals. The pictures shown in this article correspond to elements of medial rows; this is done to avoid illustration of used teeth and not yet fully formed (young) teeth. SEM images were processed in the Service Commun de Microscopie Électronique des Laboratoires des Sciences de la Vie (MNHN, Paris).

Shell: Shell descriptions are based on the holotypes and radula on holotypes, paratypes or selected specimens as noted in the text. Live collected specimens are indicated as (lv) and shells as (dd). Shell measurements are expressed in millimeters and include: length (L); maximum diameter (Max); distance of point of maximum diameter to anterior aperture (Dmax); diameter of oral aperture (Oap); maximum curvature (Arc); distance of point of maximum curvature from the apex (Larc); apical aperture diameter (Apd). For shells with oval cross-section, maximum and minimum values are included in Max and Oap. Maximum length of specimens other than the holotypes are indicated in the remarks.

Abbreviations: Institutional abbreviations used in the text are: AIM: Auckland Institute and Museum, Auckland; ANSP: Academy of Natural Sciences, Philadelphia; NHMUK: The Natural History Museum, London; IFREMER: Institute Français de Recherche pour l'Exploitation de la Mer, France; MCZ: Museum of Comparative Zoology, Harvard University; MNHN: Muséum national d'Histoire naturelle, Paris; MOM: Musée Océanographique de Monaco; QM: Queensland Museum; USNM: National Museum of Natural History, Washington, DC; WHOI: Woods Hole Oceanographic Institution, Woods Hole; SAM: South Australian Museum, Adelaide; SMHN: Naturhistoriska Riksmuseet, Stockholm; ZMB: Museum für Naturkunde, Berlin; ZMO: Zoologisk Museum, Universitetet i Oslo, Oslo; ZMUC: Zoological Museum University of Copenhagen, Copenhagen.

SYSTEMATICS

Class Scaphopoda Bronn, 1862
Order Dentaliida da Costa, 1776

Family Dentaliidae (Children, 1834)

Genus *Laevidentalium* Pilsbry and Sharp, 1897

Laevidentalium abyplaine new species
(Figures 1–5)

Description: Shell 43.3 mm long, slender, faintly curved, porcelain white, subtle longitudinal threads near apex. Sides irregularly outlined by well-defined growth lines. Cross section slightly dorsoventrally compressed in anterior 3/4, circular toward posterior aperture. Apex oblique, with ring-shape callus and lumen circular.

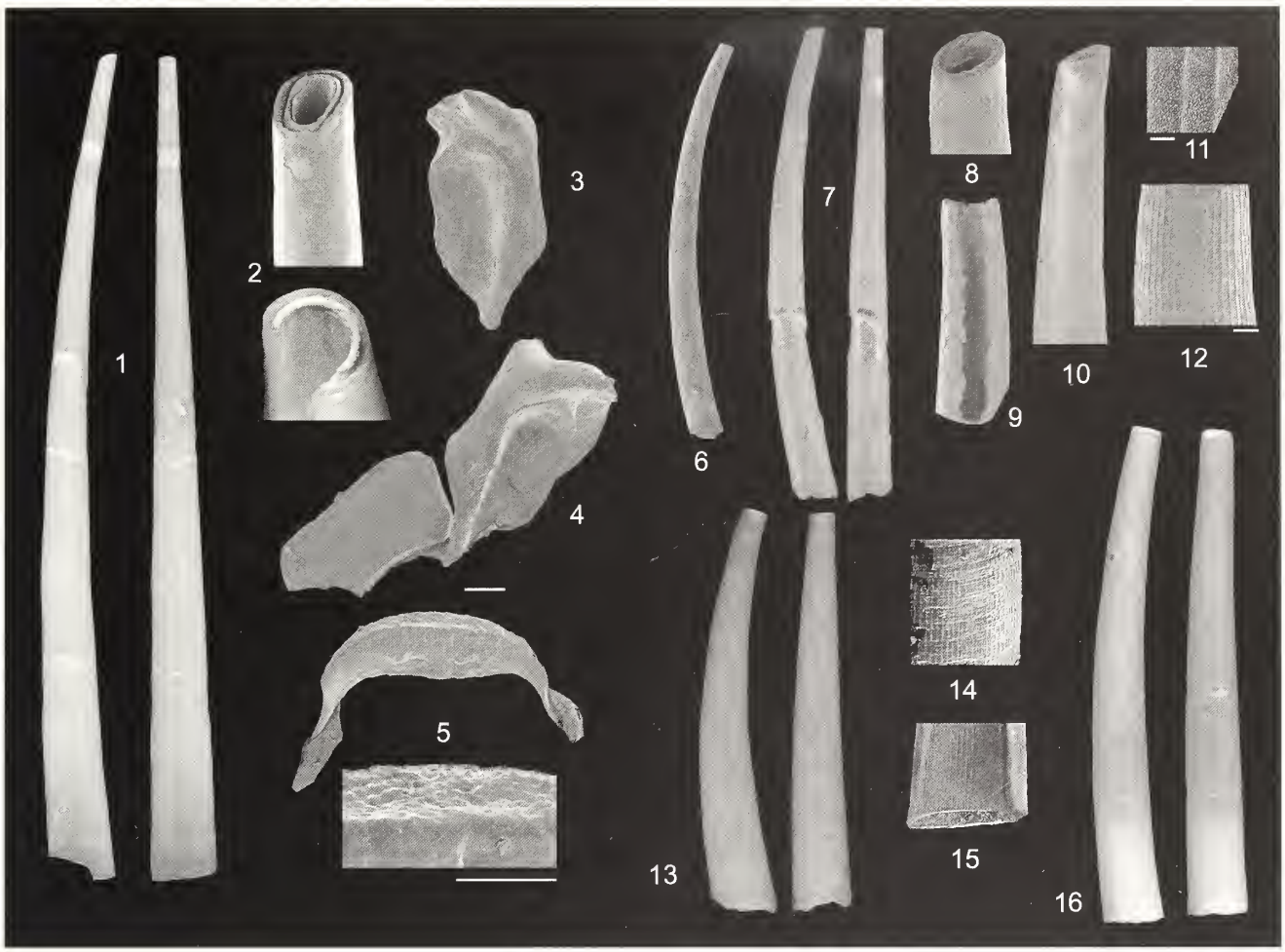
Radula (Specimen from type locality): Rachidian teeth strong, curved, with strongly granulose anterior surface; lateral teeth solid, with short but strong cusps and irregular grooves, anterior part of head smooth; marginal short almost straight.

Type Material: Holotype (lv) MNHN 24331 and 2 paratypes (lv) MNHN 24332.

Measurements of Holotype: L 43.3, Max 3.3/3.4, Apd 0.9, Arc 1.65, Larc 14.

Type Locality: Off Portugal, 39°59.5′ N, 15°00.2′ W–39°59.2′ N, 15°02.1′ W, 5330 m (Abyplaine stn CP 14).

Other Material Examined: Abyplaine, stn CP 13, 40°00.8′ N, 15°05′ W–39°59.2′ N, 15°05′ W, 5270 m, 4 dd, 1 lv; stn CP 14, 39°59.5′ N, 15°00.2′ W–39°59.2′ N, 5°02.1′ W, 5330 m, 5 lv (holotype and 2 paratypes), 12 dd; stn CP 15, 39°59.5′ N, 15°00.2′ W – 39°59.2′ N, 15°02.1′ W, 5320 m, 1 dd; stn CP 19, 43°00.1′ N, 15°53.1′ W–42°59.1′ N, 14°02.9′ W, 5280 m, 10 dd; stn CP 20, 42°59.7′ N, 14°07.2′ W–42°58.8′ N, 14°05.4′ W, 5260 m, 8 dd; stn CP 21, 42°57.7′ N, 13°59.2′ W – 42°58′ N, 14°44.0′ W, 5260 m, 5 dd; stn CP 23, 44°39.9′ N, 17°55.9′ W – 44°42.8′ N, 17°57.5′ W, 4990 m, 3 dd; stn DS 09, 40°00′ N, 15°03′ W, 5320 m, 4 dd; stn DS 10, 42°51′ N, 15°55′ W, 4360 m, 2 dd; stn DS 11, 43°00′ N, 14°05′ W, 5260 m, 4 dd; stn DS 12, 44°40′ N, 17°53′ W, 4990 m, 7 dd; stn DS 13, 44°41.2′ N, 17°49′ W, 4990 m, 6 dd. Biogas IV, stn DS 54, 46°31′ W, 10°29′W, 4659 m,



Figures 1–16. Species of *Laevidentalium*, *Pulsellum*, and *Striopulsellum*. **1–5.** *Laevidentalium abyplaine* new species. **1.** Holotype (43.3 mm), off Portugal, 39°59.5′ N, 15°00.2′ W–39°59.2′ N, 15°02.1′ W, 5330 m, ABYPLAINE stn CP14, lateral and dorsal views of shell. **2.** Details of apex, INCAL stn OS 03. **3–5.** Radula, paratype, type locality. **3.** Lateral tooth, internal view. **4.** Lateral and marginal teeth, lateral view. Scale bar = 10 µm. **5.** Rachidian tooth, anterior border and detail. Scale bar = 100 µm. **6.** *Pulsellum filiforme* new species, holotype (8.9 mm), Puerto Rico Trench, 8°12.4′ N, 55°50.2′ W, 2487–2500 m, R/V KNORR 25 stn 301, lateral view or shell. **7–12.** *Striopulsellum sandersi* new species. **7.** Holotype (7.2 mm), North Blake Plateau, 40°42.6′ N, 46°13.8′ W, 4400 m, R/V CHAIN 106, stn 334, lateral and dorsal views of shell. **8.** *Striopulsellum sandersi* new species, external view of apex. **9.** Section showing internal view. **10.** External view of apex and details of internal structure by transparency. **11.** Microsculpture of the surface. Scale bar = 10 µm. **12.** Same specimen, sculpture at center of shell. Scale bar = 100 µm. **13.** *Striopulsellum minimum* (Plate, 1908) (6.8 mm), Argentine Basin, 43°58′ S, 52°09′ W, 5781 m, R/V VEMA 1961, stn V-15-80, lateral and dorsal views. **14–15.** *Striopulsellum atlantis* new species, holotype (6 mm) off Pernambuco, Brazil, 7°58′ S, 34°17′ W, 943–1007 m, R/V ATLANTIS-II-31-167. **14.** Detail of sculpture at center of shell. **15.** Shell sculpture on oral area. **16.** *Striopulsellum knorr* new species, holotype (5.5 mm), Puerto Rico Trench, 11°2.2′ N, 55°4.8′ W, 4417–4429 m, R/V KNORR 25, stn 288; lateral and dorsal views.

1 dd. BIOGAS VI, stn CP 15, 46°32.2′ N, 10°28.5′ W, 4715 m, 1 dd; stn CP 16, 46°27.3′ N, 10°25.8′ W, 4825 m, 2 dd; stn CP 17, 46°30.8′ N, 10°19.5′ W, 4706 m, 2 lv. INCAL, stn OS 03, 46°02.5′ N, 10°19.5′ W, 4798 m, 10 dd; stn OS 04, 46°03.9′ N, 10°12.8′ W, 4796 m, 1 lv, 6 dd; stn WS 05, 46°03′ N, 10°15′ W, 4804 m, 1 dd; stn CP 12, 46°00.5′ N, 10°18.3′ W, 4796 m, 8 lv, 6 dd.

Etymology: Named (name in apposition) after the French expedition ABYPLAINE (1982) to northeastern Atlantic depths in recognition to its success on the discovery of new deep-sea species.

Distribution: Collected alive between 4796 and 5330 meters in the northeastern Atlantic Ocean off the coast of Portugal, in the Gulf of Gascony, and off northern France. *Laevidentalium abyplaine* is considered exclusively abyssal.

Remarks: Young specimens present a shallow apical notch on ventral side of apex. This feature led us to consider that the apical aspect of adult specimens is probably due to a reabsorption process. *Laevidentalium abyplaine* can be compared to *Laevidentalium leptosceles* (Watson, 1879) (Lectotype NHMUK 1887.2.9.21, examined) widely

distributed in the Indo-Pacific region in 918–5300 m depth (Scarabino, 1995). The new species is more tapering, curved and smooth, whereas *L. leptosceles* has clear longitudinal undulations, especially on the dorsal side. It also can be compared in outline to *Graptacme acutissima* (Watson, 1879) (Lectotype NHMUK 1887.2.9.31, examined) from the Indo-Pacific, but this latter has a well-defined apical notch on ventral side and longitudinal sculpture near apex. Other bathyal and abyssal Atlantic *Graptacme*, such as *Graptacme perlonga* (Dall, 1881) (Lectotype MCZ 7752, examined) is much more solid, longer, less tapering and also has apical notch and longitudinal sculpture at apex, clearly noticeable under lens. Larger specimens reach 49 mm length. *Laevidentalium abyplaine* would be the first living *Laevidentalium* recorded for the Atlantic Ocean. However, given the few conchological characters of this genus and the fact that its type species is an Eocene fossil (*Dentalium incertum* Deshayes, 1825), it is here suggested that the generic allocation of all living and fossil *Laevidentalium* should be globally reviewed.

Order Gadilida Starobogatov, 1974
Suborder Gadilimorpha Steiner, 1992
Family Pulsellidae Boss, 1982

Genus ***Pulsellum*** **Stoliezka, 1868**

Pulsellum filiforme **new species**
(Figures 6, 30–31)

Description: Shell 8.9 mm long, thread-like outline, markedly curved, arc close to middle of shell, very slow tapering. Surface irregular, translucent with white opaque patches. Apex and mouth simple, straight, section circular.

Radula (Holotype): Rachidian teeth polygonal, sides almost parallel, and anterior margin with pointed edge. Lateral teeth wide at the base and with well-armed head bearing four denticles, the two lateral teeth longer and pointed. Marginal teeth simple, straight.

Measurements of Holotype: L 8.9, Max 0.9, Apd 0.5, Arc 0.9, Larc 4.7.

Type Material: Holotype (lv) MCZ 293968, 5 paratypes (lv) MCZ 202969, 293970–73; 1 paratype (dd) MNHN 24333.

Type Locality: Puerto Rico Trench, 8°12.4′ N, 55°50.2′ W, 2487–2500 m, R/V Knorr 25 stn 301 (WHOI).

Other Material Examined: R/V Knorr 25, stn 293, 08°28.8′ N, 54°04.3′ W, 1456–1518 m, 1 lv; stn 299, 7°55.1′ N, 55°42.0′ W, 1942–2076 m, 3 lv (1 paratype), 5 dd; stn 301, 8°12.4′ N, 55°50.2′W, 2487–2500 m, 3 lv (holotype), 4 dd; R/V Knorr 35, stn 340, 38°14.4′ N, 70°20.3′ W– 38°17.6′ N, 70°22.8′ W, 3264–3356 m, 10 lv (5 paratypes), 8 dd.

Etymology: Named after the shells' narrow, "thread-like" outline.

Distribution: Collected alive between 1518–3264 meters in the Western Atlantic Ocean from the North Blake Plateau and the Puerto Rico Trench.

Remarks: The thread-like aspect with sides almost parallel and length of shell differentiate this new species from other Atlantic and worldwide *Pulsellum* species. Maximum length 9.2 mm.

Genus ***Striopulsellum*** **Searabino, 1995**

Remarks: As result of the present study, the genus *Striopulsellum* assembles six species and confirms its preference for bathyal to hadal depths worldwide. These are *Striopulsellum minimum* (Plate, 1908) (Lectotype ZMB/Moll-59728a), the type species, with circum-Antarctic distribution (3423– 6179 m depth), also recorded from New Caledonia (Scarabino, 1995) and in the Vema Basin, Argentina, live at 3423–6179 m (Scarabino, 1979, and present paper) (Figures 13, 37, specimen and radula respectively), *Striopulsellum striatinum* (Henderson, 1920) (Syntypes USNM 108106, examined) described off Fernandina, Florida, USA, from 537 m, representing the shallowest record for the genus; *Striopulsellum galatheae* Knudsen, 1964, collected alive in the Sunda Trench at 6900–7000 m depth (Holotype ZMUC), and the three new species described herein: *Striopulsellum sandersi* new species, widely distributed in the north Atlantic ocean at 3264–5800 m depth; *Striopulsellum knorr* new species in the Puerto Rico Trench at 4429–4934 m depth; and *Striopulsellum atlantis* new species, from northeastern Brazil at 943–1007 m depth.

Striopulsellum saudersi **new species**
(Figures 7–12, 36)

Description: Shell 7.2 mm long, translucent grey, regularly curved and slow tapering, arc located anterior to centre of shell. Longitudinally sculptured by 24 fine primary striae at apex and secondary ones that arise early and are doubled in number. Surface finely granulose. Apex oblique, dorsal side longer, circular in section, pre-apical callus thick. Walls of apical area alternate thinner and thicker sections, easily observed by transparency. Anterior aperture straight, circular in cross-section.

Radula (Specimen from R/V Knorr 35, stn 340): Rachidian teeth polygonal, anterior margin with three cusps, one central and two minor ones, lateral profile thicker at posterior border and thinner at anterior border, delimited by a cusp. Lateral teeth with five denticles between main cusps. Marginal teeth straight, with contact border large.

Measurements of Holotype: L 7.2, Max 0.5, Apd 0.1, Arc 0.4, Larc 4.

Type Material: Holotype (lv) MCZ 293944 and 5 paratypes: 3 (lv) MCZ 293945, 2 (lv) MNHN 24334.

Type Locality: North Blake Plateau, 40°42.6′ N, 46°13.8′ W, 4400 m, R/V Chain 106, stn 334.

Other Material Examined: R/V Chain 106, stn 334, 40°42.6′ N, 46°13.8′ W, 4400 m, 15 (holotype and 3 paratypes); R/V Knorr 35, stn 340, 38°14.4′ N, 70°20.3′ W, 3264–3356 m 3 lv; Abyplaine, stn CP 21, 42°57.7′ N, 13°59.2′ W - 42°58′ N, 14°44.0′ W, 5260 m, 1 lv; stn DS 04, 34°54′ N, 21°26.10′ W, 5160 m, 1 lv, 1 dd; stn DS 06, 32°03′ N, 22°01′ W, 5250 m, 1 lv; stn DS 10, 42°51′ N, 15°55′ W, 4270–4360, 3 dd; stn DS 11, 43°00′ N, 14°05′ W, 5260 m, 2 lv (paratypes). Biogas VI, stn 10-CB5, 55°43′ N, 49°21′ W, 3676 m, 1 lv; stn 19-CB8, 38°55, 46°47′ W, 5320 m, 5 lv, 2 dd; stn 78, 46°31′ N, 10°24′ W, 4706 m, 1 lv; stn 79, 44°30′ N, 10°27′ W, 4715 m; Biovema, stn 09, 11°36′ N, 32°52′ W, 5875 m 32 lv; stn CP 22, 44°42′ N, 17°59′ W, 1 lv; stn DS 04 34°54′ N, 21°26′ W, 5160 m, 10 lv; stn DS 06, 32°03′ N, 22°01′ W, 5250 m, 2 lv; 2 dd; stn DS 10, 11°33′ N, 32°52′ W, 5875 m, 3 lv; stn DS 11, 43°00′ N, 14°05′ W, 5260 m, 2 lv; Noratlante, 1969, stn 21, 38°28′ N, 3°03′ W, 5228–5240 m, 2 lv; stn DS 08, 52°10′ N, 45°32′ W, 4100–4120, 1 lv; stn DS 19, 38°55′ N, 46°47′ W, 5320, 2 lv.

Etymology: Named after the late Dr. Howard L. Sanders (WHOI), contemporary pioneer of deep-sea zoological research of the Atlantic Ocean, who hosted the senior author in his laboratory at Woods Hole, many years ago, and made available for study several of the specimens described in the present paper.

Distribution: Collected alive between 3264–5800 meters from the North Atlantic basin, Vema Trench and the Gulf of Gascony.

Remarks: Compared to the other two new species described here, *Striopulsellum sandersi* new species is more regularly curved than *S. knorr* new species and *S. atlantis* new species, has the apex oblique and it is specially identified by the characteristic structure of the wall on the apical area. Shells frequently present breakages and repairs. Maximum length 11.3 mm.

***Striopulsellum knorr* new species**
(Figures 17, 34–35)

Description: Shell 5.5 mm long, translucent grey, slightly curved and slow tapering. Longitudinally sculptured by 34 fine but well-defined primary striae, secondary ones appearing on posterior quart, doubling in number. Apex straight, circular in cross-section, apical callus thick, lumen circular. Mouth straight, circular in section.

Radula (Holotype): Rachidian teeth polygonal, anterior margin with single cusp. Lateral teeth with four denticles between main cusps. Marginal teeth slightly curved.

Measurements of Holotype: L 5.5, Max 0.6, Apd 0.2, Arc 0.3, Larc 2.2.

Type Material: Holotype (dd) MCZ 293947 and 6 paratypes (2 lv, 1 dd) MCZ 293948, (3 dd) MCZ 293949.

Type Locality: Puerto Rico Trench, 11°2.2′N, 55°4.8′W, 4417–4429 m (R/V Knorr 25, stn 288).

Material Examined: Puerto Rico Trench, R/V Knorr 25, stn 287, 13°15.8′N, 54°52.2′W, 4934–4980 m (3 paratypes, dd); stn 288, 11°02.2′N, 55°4.8′W, 4417–4429 m (holotype and 3 paratypes, 2 lv, 1 dd).

Etymology: Named (name in apposition) after the R/V Knorr (WHOI).

Distribution: Puerto Rico Trench, collected alive in 4429–4934 m.

Remarks: When compared to the other congeners, *Striopulsellum knorr* is almost straight, its apical callus is thicker, and the striae are less evident.

***Striopulsellum atlantis* new species**
(Figures 7, 14–15, 32–33)

Description: Shell 6 mm, slender, slightly curved, fragile, translucent grey. Apical area smooth, with 72 fine striae, appearing early and covering the remainder of shell. Spaces between striae convex and surface roughly granulose. Apex simple, preapical callus thin.

Radula (Holotype): Rachidian teeth polygonal, anterior border irregular. Head of lateral teeth with four denticles between the three main cusps, in number of two in the internal side and one more pointed on external side of teeth head. Marginal teeth slightly curved, thicker at contact points with laterals.

Measurements of Holotype: L 6, Max 0.75, Apd 0.3, Arc 0.2, Larc 3.1.

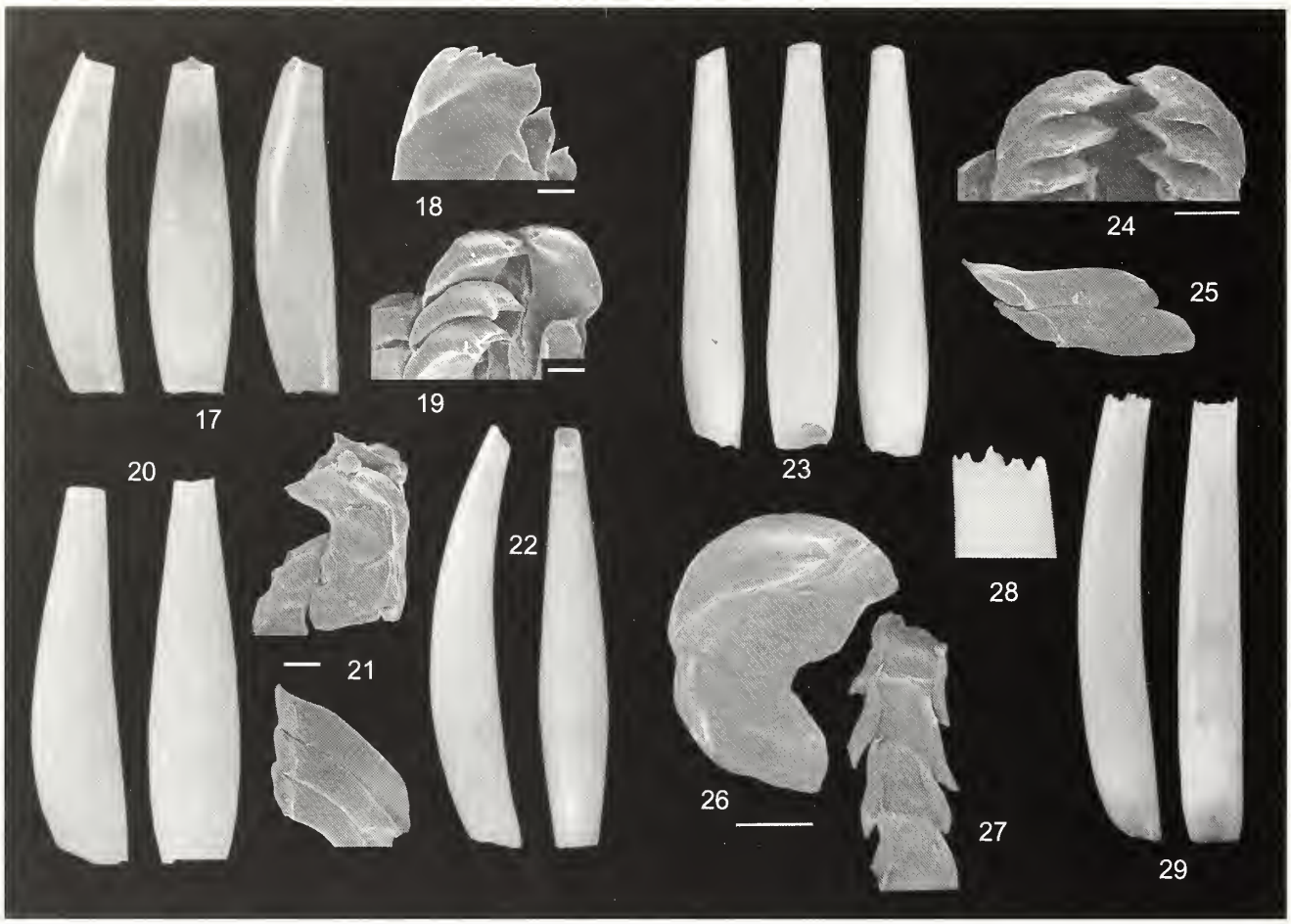
Type Material: Holotype (lv): MCZ 293950; paratypes (2 lv) MCZ 293951.

Type Locality: Off Pernambuco, Brazil, 7°58′ S, 34°17′ W, 943–1007 m (R/V Atlantis-II-31-167).

Other Material Examined: Off Pernambuco, Brazil, R/V Atlantis II-31-167, 7°58′ S - 34°17′ W, 943–1007 m, 3 lv.

Etymology: Named (name in apposition) after the R/V Atlantis II (WHOI).

Distribution: Know only from the type locality. Collected alive at 943–1007 m.



Figures 17–29. Speeies of *Cadulus*, *Gadila*, *Chistikovia*, and *Siphonodentalium*. **17–19.** *Cadulus unilobatus* new speeies, holotype (4 mm), Gulf of Gascony, 47°36.1′ N, 8°40.5′ W, 2360 m, BIOGAS V stn DS 65. **17.** *Cadulus unilobatus* new speeies, holotype (4 mm), Gulf of Gascony, 47°36.1′ N, 8°40.5′ W, 2360 m, BIOGAS V stn DS 65, lateral, dorsal and ventral views. **18.** *Cadulus unilobatus* new species, paratype, radula, details of the head of lateral teeth, internal view (bar10 mμ). **19.** Radula, external view of lateral, raehidian, and head or marginal teeth. Seale bar = 10 μm. **20, 21.** *Gadila cretea* new speeies, holotype (5.5 mm), off Fernando de Noronha, Brazil, 00°3′ S, 27°48′ W, 3730–3787 m, R/V Atlantis II-31 stn 155, lateral and dorsal views. **20.** *Gadila cretea* new species, radula, Gulf of Gascony, 47°27.30′ N, 9°39.9′ W, 4354 m, Incal, stn WS10, internal view of lateral and rachidian teeth. Seale bar = 10 μm. **21.** *Gadila cretea* new species, radula, same locality as of speeimen in Figure 20, internal view of marginal teeth. Seale bar = 10 μm. **22.** *Gadila celtica* new speeies, holotype (10.6 mm), Gulf of Gaseony, 47°32.5′ N, 9°04.1′ W, 2813 m, BIOGAS II stn DS 31, lateral and dorsal views. **23–25.** *Chistikovia atlantica* new speeies, holotype (16.9 mm), North Blake Plateau, 40°42.6′ N, 46°13.8′ W, 4400 m, R/V Chain 106 stn 334. **23.** Lateral, ventral and dorsal views of the shell. **24.** Radula, external view of lateral teeth heads and raehidian teeth. **25.** Internal view of marginal teeth. **26–29.** *Siphonodentalium coronatum* new speeies. **26.** Paratype, radula, internal view of lateral tooth, **27.** Rachidian teeth, internal view. Seale bar: 100 μm. **28.** Details of shell apex. **29.** Holotype (16.1 mm), North Blake Plateau 40°42.6′ N, 46°13.8′ W, 4400 m R/V Chain 106, stn 334, lateral and dorsal views.

Remarks: *Striopulsellum atlantis* differs from its eongeners by the absence of sculpture at apical seetor and less noticeable striae.

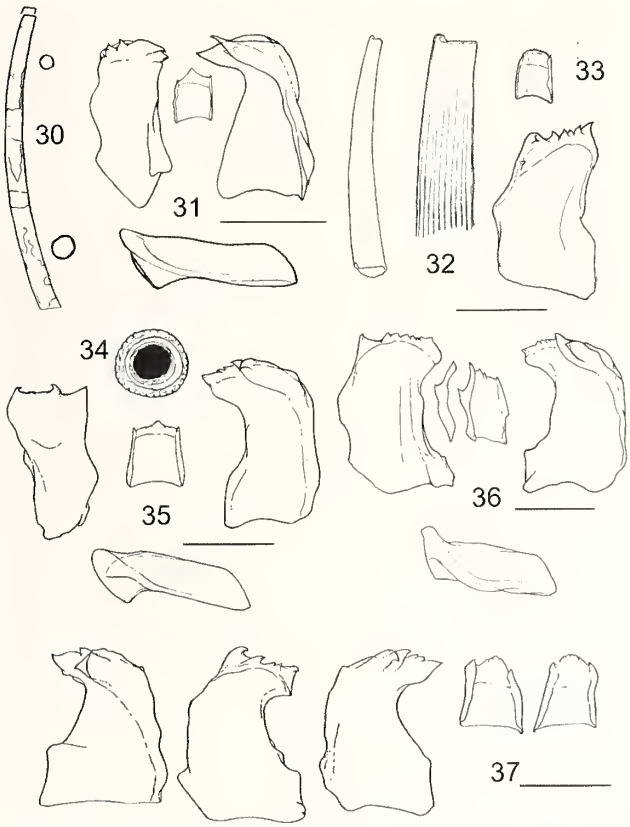
Subfamily Gadilinae Stoliczka, 1868

Genus ***Cadulus* Philippi, 1844**

***Cadulus unilobatus* new species**
(Figure 17–19)

Description: Shell 4 mm long, transhcent white, maximum diameter at anterior third of shell. In lateral view, ventral side is regularly eurved to apex, whereas dorsal side shows very slightly concave and eonvex alternating lines. In frontal view, sides are almost straight, from maximum diameter to apex and to mouth. Growth lines well-defined, straight. Apex wide, slightly dorsoventrally eompressed, with small, rounded edge lobe on ventral side. Preapieal eallus thick, lumen dorsoventrally oval. Anterior aperture straight, slightly dorsoventrally eompressed.

Radula (Paratype): Rachidian teeth polygonal, anterior border with small medial pointed process. Lateral teeth strong, surfaee of head irregular, with three main cusps, two of whieh are located on internal area and third



Figures 30–37. Species of *Pulsellum* and *Striopulsellum*. **30–31.** *Pulsellum filiforme* new species. **30.** Lateral view and apical and oral profiles. **31.** Radula of holotype, left, lateral teeth, internal face; right, lateral faces; center, rachidian tooth; below, marginal teeth. Scale bar = 100 μm. **32–33.** *Striopulsellum atlantis* new species, holotype (6 mm), off Pernambuco, Brazil, 7°58′ S, 34°17′ W, 943–1007 m, R/V Atlantis-II-31-167], lateral view and details of apical area. **33.** Holotype, radula, above, rachidian tooth; below, lateral tooth, internal view. Scale bar = 100 μm. **34–35.** *Striopulsellum knorr* new species, holotype (5.5 mm), Puerto Rico Trench, 11°2.2′ N, 55°4.8′ W, 4417–4429 m, R/V Knorr 25, stn 288. **34.** Apex in cross-section. **35.** Left, external view of lateral tooth; center, rachidian tooth; right, lateral tooth, internal view; below, marginal tooth. Scale bar = 100 μm. **36.** *Striopulsellum sandersi* new species, radula, R/V Knorr 35, stn 340, left, lateral tooth, external view; right, lateral tooth; center, internal view; rachidian, lateral and internal views; below, marginal tooth (bar: 100 mμ). **37.** *Striopulsellum minimum* (Plate, 1908), radula, left, views of lateral teeth; right, internal views of rachidian teeth.

cusp wide and small, external pointed cusp. Between cusps, four denticles of different sizes, placed at different angles between cusps. Marginal teeth slightly curved with thicker contact point with laterals.

Measurements of Holotype: L 4, Max 1/0.9, Dmax 1.2, Oap 0.66/0.6, Apd 0.4/0.35, Arc 0.14, Larc 1.5.

Type Material: Holotype (lv) MNHN 24335 and 2 paratypes (lv) MNHN 24336.

Type Locality: Gulf of Gascony, 47°36.1′ N, 8°40.5′ W, 2360 m (BIOGAS V stn DS 65).

Other Material Examined: BIOGAS V, stn DS 65, 47°36.1′ N, 8°40.5′ W, 2360 m, 10 lv (including holotype and 2 paratypes), 3 dd.

Etymology: Only one lobe, to highlight the apical feature.

Distribution: Known only from the type locality, collected alive in 2360 m depth.

Remarks: Relative location of the maximum diameter and the ventral apical lobe distinguishes *Cadulus unilobatus* from other congeners reported to the area such as *C. artatus* Locard, 1897 (holotype not located), *C. gracilis* Jeffreys, 1877 (holotype USNM 175853, examined), *C. jeffreysi* (Monterosato, 1875) (type material not located), *C. propinquus* G. O. Sars, 1878 (syntypes ZMO 26071–72), and *C. subfusiformis* M. Sars, 1865 (syntypes SMNH 4626). Other species presenting similar apical structure to *Cadulus unilobatus* are *C. teliger* Finlay, 1926 (Tertiary of New Zealand) from New Zealand (holotype AIM; paratypes ANSP 232249; DMNH 22370, examined), *C. vincentianus* Cotton and Godfrey, 1940, from the eastern Australia (Holotype, SAM D13730), and an undescribed species from the Philippines.

Genus ***Gadila* Gray, 1847**

***Gadila cretea* new species**
(Figure 20–21)

Description: Shell 5.5 mm long, opaque chalky-white, fragile. Maximum diameter on anterior third. Dorsal side almost straight, ventral evenly convex on anterior three-fourths of shell, straight to apex. In dorsal view, sides present outline similar to ventral. Apex large, simple, circular in section, callus thick. Oral aperture oblique, slightly compressed laterally. Growth lines oblique.

Radula (Incal: stn DS16, stn WS10): Rachidian teeth, with large sides and pointed medial cusp. Lateral teeth with two pointed processes on internal face and another on outer side, space in between with 8 denticles, external face of the head irregular. Marginal teeth slightly curved, keeled.

Measurements of Holotype: L 5.5, Dmax 1.6, Oap 0.7, Apd, 0.5. Arc 0.1, Larc 2.3.

Type Material: Holotype (lv) MCZ 293933 and 4 paratypes: 2 (lv), MCZ 293935, 193936; 2 (lv) MNHN 24337.

Type Locality: Off Fernando de Noronha, Brazil, 00°3′ S, 27°48′ W, in 3730–3787 m (R/V Atlantis II-31 stn 155).

Material Examined: R/V Atlantis II-31, stn 155, 0°3′ S, 27°48′ W, 3730–3787 m, 6 lv (holotype and 5 paratypes); Biaçores: stn 126, 39°19.5′ N, 33°47.0′ W, 3360 m, 4 dd; R/V Knorr 35, stn 340, 2 lv; 39°19.5′ N, 33°47′ W, 3360 m, 1 lv; R/V Chain 106, stn 334, 40°42.6′ N, 46°13.8′ W, 4400 m, 1 lv (paratype); stn 234, 38°14.4′ N, 70°20.3′ W–38°17.6′ N, 70°22.8′ W, 3264–3356 m 1 lv (paratype); Incal, stn DS16, 47°29.8′ N, 9°33.4′ W, 4268 m, 2 lv, 1 dd; stn WS09, 47°28.80′ N, 9°34′ W, 4277 m, 1 lv 2 dd; stn WS10, 47°27.30′ N, 9°39.9′ W, 4354 m, 3 lv, 1 dd; stn DS15, 47°33.40′ N, 9°39.10′ W, 4211 m, 1 lv, 2dd. Biogas IV, stn DS55, 47°34.9′ N, 9°40.9′ W, 4125 m, 16 lv (2 paratypes), 18 dd; Biogas V, stn DS66, 47°28.20′ N, 9°00′ W, 3480 m, 2 d; stn 67, 47°31′ N, 9° 35′ W, 4510 m, 1 lv; Biogas VI, stn DS75 47°28.1′ N, 9°07.8′ W, 3250 m, 1 lv 2 d; stn DS76, 47°34.8′ N, 9°33.3′ W, 4228 m, 17 lv, 2 dd; stn DS77 47°31.8′ N, 9°34.6′ W, 4240 m, 2 lv.

Etymology: From Latin *creteus*, chalk, referring to the surface texture on shells of this species.

Distribution: Live collected between 3264–4510 meters. Its range is amphi-Atlantic. In the Western Atlantic it is found in the Pernambuco Basin and Puerto Rico Trench, in Eastern Atlantic basins from the Gulf of Gascony to the Azores.

Remarks: According to its unusual shell outline, there is no similar species in the Atlantic Ocean to be compared with *G. cretea*. Maximum length 5.8 mm.

***Gadila celtica* new species**
(Figure 22)

Description: Shell 10.6 mm long, gently curved, and tapering, polished white. Maximal diameter at anterior third. Ventral side regularly curved, dorsal side alternating concave and convex outline. Apex simple, clearly oblique, ventral side longer, slightly laterally compressed. Apical callus thin. Mouth slightly oblique, laterally compressed. Growth lines easily noticeable, also oblique. Radula unknown.

Measurements of Holotype: L 10.6, Dmax 1.7/1.9, Oap 1/1.1, Apd 0.5, Arc 0.33, Larc 4.1.

Type Material: Holotype (dd) MNHN 24338 and 3 paratypes (1 lv, 2 dd). MNHN 24339.

Type Locality: Celtic Sea, 47°32.5′ N, 9°04.1′ W, 2813 m (Biogas II, stn DS 31).

Material Examined: Biogas II, stn DS 31, 47°32.5′ N, 9°04.1′ W, 2813 m, 1 dd (holotype). Biogas III stn DS 38, 47°32.5′ N, 8°35.8′ W, 2138 m, 2 dd (paratypes); Biogas V, stn DS 65, 47°36.1′ N, 8°40.5′ W, 2360 m, 1 lv (paratype).

Etymology: Named after the Celtic Sea, general area of the type locality.

Distribution: Collected alive in 2360 meters, with dead shells found between 1913–2813 meters. A North Atlantic Ocean species known from the Northeastern Celtic Sea and the Gulf of Gascony.

Remarks: *Gadila celtica* can be compared to *G. miamiensis* (Henderson, 1920), from off Florida (USA) in 209 fms (382 m) (holotype USNM 314772, examined) and *G. bushii* (Dall, 1889) from Barbados in 100 fms (182 m) (lectotype MCZ 7745, examined). Individuals of both species are smaller than *G. celtica* and have a straight apex. *Gadila miamiensis* has the most similar outline, but is more curved and the oral profile is more oblique than *G. celtica*, and *G. bushii* clearly tapers faster and the apical area is narrower.

Family Wemersoniellidae Scarabino, 1986

Genus ***Chistikovia* Scarabino, 1995**

***Chistikovia atlantica* new species**
(Figure 23–25)

Description: Shell 16.9 mm long, porcelain white, solid, almost straight and clearly dorsoventrally depressed. Maximum diameter near the oral aperture from where the shell tapers regularly to apex and mouth. Unsculptured, except for very oblique, conspicuous, and close-set growth lines. Apex wide, margin very oblique, dorsal side higher, callus thick. Mouth thin walled, oblique.

Radula (Holotype): Rachidian teeth polygonal with anterior margin simple. Lateral teeth strong, with a sharp pointed primary cusp with irregular grooves on the outer part of the head. Marginal teeth almost straight, pointed at inner margin.

Measurements of Holotype: L 16.9, Max 2.5/2.9, Dmax 4.4, Oap,1.8/1.5, Apd 1-1.3.

Type Material: Holotype (lv) MCZ 293927 and 5 paratypes (1 lv, 4 dd): 3 MNHN 24340 (1 lv, 2 dd); 1 ZMUC (dd); 1 (dd) MOM 291146.

Type Locality: North Blake Plateau, 40°42.6′ N, 46°13.8′ W, 4400 m (R/V Chain 106, stn 334).

Material Examined: R/V Chain 106, stn 334, 40°42.6′ N, 46°13.8′ W, 4400 m (1 lv, holotype); Biogas III: stn CV 23, 47°32.7′ N, 8°34.2′ W, 2034 m, 1 dd; Biogas IV, stn DS 55, 47°34.9′ N, 9°40.9′ W, 4125 m, 1 lv; Biogas V, stn DS 66, 47°28.2′ N, 9°00′ W, 3480 m, 2 lv, 1 dd; Biogas VI, stn DS 75, 47°28.1′ N, 9°07.8′ W, 3250 m, 1 dd; stn DS 76, 47°34.8′ N, 9°33.3′ W, 4228 m, 1 lv, (paratype) 1 dd; Incal, stn DS 10, 50°12.7′ N, 13°16.6′ W, 2719 m, 1 dd

(paratype); stn DS 15, 47°33.4′ N, 9°39.1′ W, 4211 m, 1 dd (paratype); stn WS 07, 55°00.7′ N, 12°31′ W, 2884 m, 1 dd. Noratlante, stn 10 CB5, 55°43′ N, 49°21′ W, 3876 m, 1 dd; R/V Princesse-Alice II (1911), stn 2964, 46°17.30′ N, 05°42′ W, 4387 m, 1 dd (paratype); Incolf (1895), stn 38, 59°12′ N, 51°05′ W, 3521 m, 1 dd (paratype).

Etymology: Relative to the Atlantic Ocean.

Distribution: Collected alive between 3250–4400 meters, dead shells found between 2034–4400 meters. A North Atlantic Ocean species found off the southwest and south coast of Greenland, high latitudes of the central and northeastern Atlantic, off Ireland and the Gulf of Gascony.

Remarks: The other species of this genus are *Chistikovia kermadecae* Scarabino, 1995 (the type species) from Kermadec Trench, New Zealand in 2470–4570 m (holotype ZMUC, 11.5 mm), and *Chistikovia earlessi* (Lamprell and Healy (1998), as *Gadila earlessi*) from northern Queensland, Australia, in 2710 m, (holotype QM MO40084, 19.2 mm). *Chistikovia atlantica* is similar to *C. earlessi*, the main difference being the location of the maximum diameter, clearly more anterior in the latter than in the new species. *Chistikovia kermadecae* has the ventral side slightly curved, not straight as in *C. atlantica* and *C. earlessi*, and, in addition, the apical structure is better defined.

Family Siphonodentaliidae Simroth, 1894

Genus ***Siphonodentalium* M. Sars, 1859**

***Siphonodentalium coronatum* new species**
(Figure 26–29)

Description: Shell 16.1 mm long, slightly curved, brilliant white, fragile. Maximal diameter near oral aperture, gradually tapering to apex. Ventral side regularly convex, dorsal side regularly concave from maximum diameter to apex, almost straight to mouth. Apex notably large, crown-like, with 12 lobes, five each on dorsal and ventral sides and two lateral, higher and sharper due to deep latero-ventral notches. Oral aperture oblique, slightly dorsoventrally depressed.

Radula (Paratype, MNHN 24341): Rachidian teeth with one cusp on lateral sides and three smaller ones on anterior side, two of which ventrally placed and one centro-dorsally placed. Lateral teeth with large anterior third, curved, with two pointed processes on dorsal face and one smaller on one side and another on other side, with smooth intervening gap. Marginal teeth straight.

Measurements of Holotype: L 16.1, Max 2.5, Oap 2.0/1.9, Dmax 4.8, Apd 1.6, Arc 0.6, Larc 7.2.

Type Material: Holotype (lv) MCZ 293926 and 2 paratypes (lv) MNHN 24341.

Type Locality: North Blake Plateau, 40°42.6′ N, 46°13.8′ W, 4400 m (R/V Chain 106, stn 334).

Other Material Examined: R/V Chain 106, stn 334, 40°42.6′ N, 46°13.8′ W, 4400 m, (lv) holotype; Biogas II, stn DS 23, 46°32.8′ N, 10°21′ W, 4734 m, 1 lv (paratype); Biogas V, stn DS 69, 44°21.9′ N, 4°52.4′ W, 4510 m, 1 lv (paratype); stn DS 82, 44°25.4′ N, 4°52.2′ W, 4462 m, 1 lv; stn CP 19, 44°24.9′ N, 4°51.3′ W, 4434 m 1 lv; Incal, stn WS 08, 47°30.5′ N, 9°32.9′ W, 4287 m, 1 dd.

Etymology: Specific epithet refers to the crown-like shape of the apex.

Distribution: Collected alive between 4510–4734 meters, dead shells from 4287 meters. A North Atlantic Ocean species found southwest of Ireland, the Gulf of Gascony and off Portugal.

Remarks: Three other species of *Siphonodentalium* are cited for the northeastern Atlantic: *Siphonodentalium lobatum* (Sowerby, 1860) (syntypes NHMUK 1951.2.14.4–5, examined), *Siphonodentalium laubieri* Bouchet and Warén, 1979 (holotype and paratypes at MNHN, examined), and *Siphonodentalium spectabilis* (Verrill, 1885) (lectotype USNM 37935, examined). The first species is more curved and tapering than the new species, and *S. laubieri* has only four lobes and notches. *Siphonodentalium laubieri* is known only from the Norwegian Sea and the Laptev Sea in 2212–2502 m depth (Sahlmann et al., 2009), whereas *S. lobatum* has a large geographic and bathymetric distribution in the northern Atlantic from off British Islands to Spitzbergen, Arctic Sea and Barents Sea in 38–3100 m depth (Ivanov and Zarubina, 2004). *Siphonodentalium spectabilis* (Verrill, 1885), occurs in the northwestern Atlantic at 2780 m depth and has amphi-Atlantic distribution; it is much more tapering that the other species and have distinct arrangement and size of apical lobes.

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A new genus of Cretaceous margaritine gastropod (Turbinidae) from the northeastern Pacific Ocean

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ABSTRACT

Igonoia, a new genus of a margaritine vetigastropod, is recognized from Lower and Upper Cretaceous rocks in the northeastern Pacific, in the region extending from Vancouver Island, British Columbia, to southern California. Eight species are known, five are new: the early late Albian *I. kieli* new species and *I. shastana* new species; the late Cenomanian *I. onoensis* new species and *I. stewarti* (Murphy and Rodda, 1960) new combination; the late Turonian *I. vacca* new species; the Santonian *I. occidentalis* (Whiteaves, 1903) new combination; and the Maastrichtian *I. angulata* (Gabb, 1869) new combination and *I. muiri* new species. *Igonoia* is presently known to be endemic to the study area. Specimens are found predominantly in northern California, in fine-grained siliciclastic sandstones that were deposited in warm-temperate, shallow-marine waters. Specimens are most numerous in Santonian rocks.

Additional keywords: Mollusca, Margaritinae, fossil, endemic, temperate waters

INTRODUCTION

Small trochiform vetigastropods present in Cretaceous shallow-marine rocks of the northeastern Pacific are poorly documented in the literature. In the author's ongoing process of attempting to establish which genera are present, a new genus of margaritine vetigastropod was detected in museum collections. The new genus *Igonoia* occurs in both Lower and Upper Cretaceous shallow-marine rocks in the region extending from Vancouver Island, British Columbia, Canada to southern California. Specimens are locally abundant but are otherwise uncommon faunal elements. There are eight known species of the new genus, and five of them are new. The three previously named ones were originally assigned to other similar-looking genera. In addition to erecting the new genus, the main purposes of this paper are to describe its species and to record their biostratigraphic succession. The areas where the specimens were collected are shown on Figure 1, and their designations (e.g., Area 3) are used throughout the paper. The details of the type localities of the species are given in the Appendix. The temporal distributions of the species are shown in Figure 2. Paleogeographic and paleoclimatic conditions of the new genus are discussed.

Included in this paper are supplementary descriptions (based on new examination of type material) and refined biostratigraphic records of the three previously named species: *Igonoia angulata* (Gabb, 1869); *Igonoia occidentalis* (Whiteaves, 1903); and *I. stewarti* (Murphy and Rodda, 1960). New information about the type locality of *I. angulata* is provided, and its type material consists of two species: *I. angulata* and *I. muiri* new species. The first photographic views of the type material of *I. occidentalis* are provided. Additional photographic views of *I. stewarti* are given, and its type material consists of two species: *I. stewarti* and *I. ononensis* new species.

This study was based on 260 specimens borrowed from museums having extensive collections of northeast Pacific Cretaceous fossils. Most of the specimens are stored in the Invertebrate Paleontology Collection at the Natural History Museum of Los Angeles County. The base and umbilical areas of the specimens are commonly encased in well-cemented, fine-grained siliciclastic sandstone. In order to remove this material, it was necessary to use a high-speed drill and diamond-coated grinding wheels, followed by the careful use of hand-held, very sharp needles. Preservation of shell material is generally good. Protoconch and early teleoconch whorls are very rarely present, and mostly or completely decollated. The one moderately well preserved protoconch with its shell intact was sputter-coated

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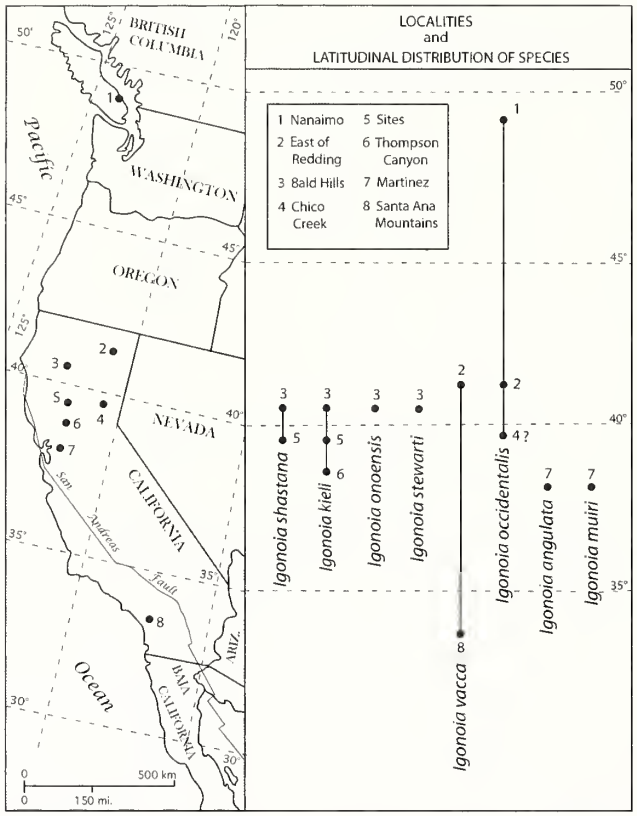


Figure 1. Localities map and latitudinal distribution of study area species of *Igonoia*.

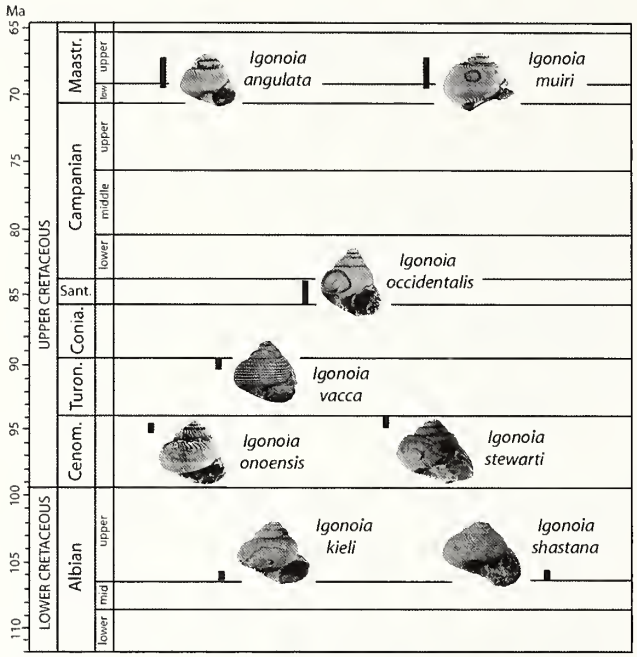


Figure 2. Geologic ranges of the studied species of *Igonoia*. Ages of stage boundaries from Gradstein et al. (2004).

prior to being imaged by means of an Hitachi S-3000N SEM (scanning electron microscope).

Abbreviations used for catalog and locality numbers are: ANSP: Academy of Natural Sciences, Philadelphia; GSC: Geological Survey of Canada, Ottawa; LACMIP: Natural History Museum of Los Angeles County, Invertebrate Paleontology; UCLA: University of California, Los Angeles (collections now housed at LACMIP); USGS: United States Geological Survey, Menlo Park, California (collections now housed at University of California, Berkeley, Museum of Paleontology).

SYSTEMATIC PALEONTOLOGY

Clade Vetigastropoda Salvini-Plawen, 1980
Family Turbinidae Rafinesque, 1815
Subfamily Margaritinae Stoliczka, 1868

Remarks: This subfamily was previously generally believed to be a trochid subfamily (e.g., Fretter and Graham, 1977; Hickman and McLean, 1990), but, based on molecular studies of extant taxa by Williams et al. (2008), it has been recently and provisionally recognized to be a turbinid. Williams et al. (2009) demonstrated that Margaritinae is not monophyletic.

Genus *Igonoia* new genus

Type Species: *Igonoia onoensis* new species, late Cenomanian, northern California.

Description: Shell size very small to medium small (4.5 to 13 mm height). Shell height commonly slightly less or approximately same size as shell diameter, rarely greater than diameter. Trochiform. Phaneromphalous. Spire low to moderately high, 43% to 59% of shell height. Pleural angle 80° to 95°. Protoconch smooth (most likely less than one whorl), transition to teleoconch unclear. First teleoconch whorl showing spiral threads before showing any axial ribs. Teleoconch four to six convex whorls; base usually rounded. Suture sunken and commonly groove-like. Teleoconch ornament of spiral ribs (beaded or unbeaded), commonly crossed by raised growth lines, especially on ramp/shoulder areas; shells can be nearly smooth. Shoulder rounded. Aperture circular. Peristome discontinuous. Last whorl large, base convex or keeled. Umbilicus open and deep, bounded by beaded weak to moderately strong spiral rib; umbilical wall can have cancellate ornament where growth lines intersect spiral ribs.

Geologic Age: Early late Albian to "mid" Maastrichtian (early late to late middle).

Etymology: Named for the adjacent towns of Igo and Ono in the Bald Hills area, Shasta County, northern California.

Remarks: After careful examination of each specimen, only two were found with remnants of their protoconch

present. Only one of these, a specimen of *I. onoensis* (Figures 21–22), has the shell intact on its protoconch, whereas the other, a specimen of *I. shastana* (Figure 14), is missing its shell on the protoconch and adjacent early teleoconch whorls (only an internal mold is present).

Gabb (1869) originally assigned the material that is now known to comprise *I. angulata* (Gabb, 1869) and *I. muiri* new species to genus *Margaritella* Meek and Hayden, 1860, a *nomen dubium* (not *Margaritella* Thiele, 1891).

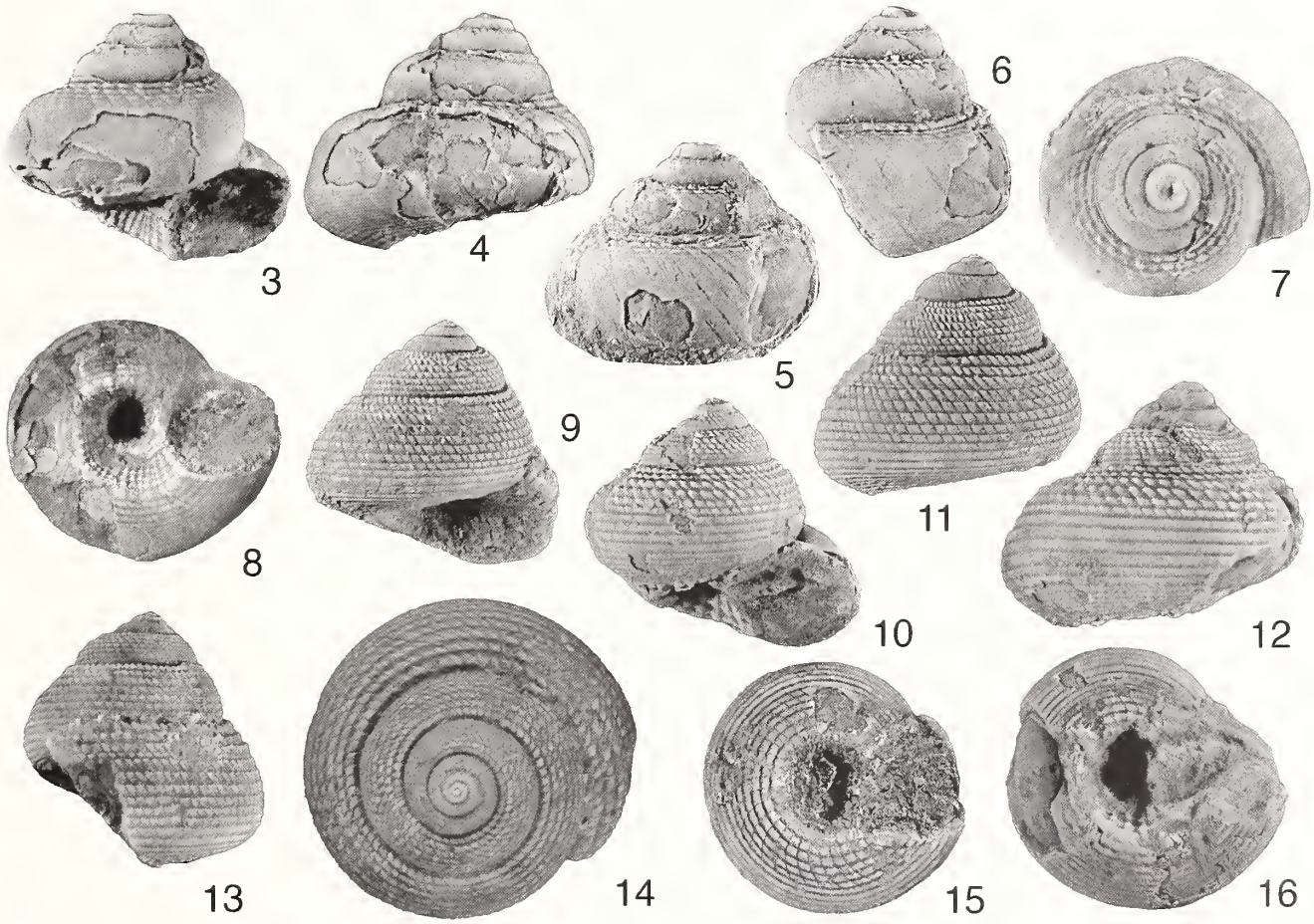
The other previously named species of *Igonoia* were assigned eventually by other workers (Whiteaves, 1903; Stewart, 1927; Murphy and Rodda, 1960) to the solarielline genus *Solariella* Wood, 1842. This is not surprising, given that Hickman and McLean (1990) reported that solariellines are known to have produced convergences with margaritine shells. Fossil species of *Solariella* have been characterized (e.g., Davies, 1971; Kiel and Bandel, 2001) as having a continuous peristome, spiral cords that can be strongly noded, a keel on the base of the shell, and a very prominent spiral cord on the rim of the umbilicus. *Igonoia* differs from *Solariella* by having a discontinuous peristome, sunken suture, shoulder with raised growth lines with or without axially aligned beads, whorl sides with or without axially aligned beads, and commonly an absence of a very prominent spiral rib bordering the umbilicus.

Igonoia is similar to genus *Margarites* J. E. Gray, 1847 (ex Leach ms), but *Igonoia* differs by having a ramp or shoulder with raised growth lines with or without axially aligned beads, whorl sides with or without axially beads, and commonly a less prominent spiral rib bordering the umbilicus.

Igonoia kieli new species
(Figures 3–8)

Diagnosis: Small-sized *Igonoia*, ramp slightly concave, moderately wide, and bearing up to three beaded spiral ribs (posteriormost ones more prominent); whorl sides smooth or with some prominent growth lines present and extending posteriorward across ramp.

Description: Shell size small (up to height 8 mm, diameter 9 mm, same specimen). Shell height



Figures 3–16. Albian species of *Igonoia* new genus. Specimens coated with ammonium chloride. **3–8.** *Igonoia kieli* new species. **3–7.** Holotype LACMIP 13682, LACMIP loc. 22900, height 8.7 mm, diameter 9.4 mm. **8.** Paratype LACMIP 13683, LACMIP loc. 22900, height 6.6 mm, diameter 8.4 mm. **9–16.** *Igonoia shastana* new species. **9, 11, 13, 14, 15.** Holotype LACMIP 13684, LACMIP loc. 28757, height 6.3 mm, diameter 6.2 mm. **10, 12, 16.** Paratype LACMIP 13685, LACMIP loc. 24369, height 7.5 mm, diameter 8.1 mm.

approximately 92% of shell diameter. Trochiform. Phaneromphalous. Spire moderately elevated, approximately 54% of shell height. Pleural angle approxiately 87°. Protoconch unknown. Teleoconch approximately five convex whorls. Suture impressed. Ramp slightly concave and moderately wide. Upper spire whorls with two subsutural and equal-strength beaded spiral ribs; penultimate whorl with three beaded spiral ribs, all nearly equal strength. Ornament on last whorl with six spiral ribs, posteriormost two beaded (elongate beads) and equal strength, anteriormost four ribs unbeaded and weaker strength. Ornament on whorl sides obsolete or with some widely spaced, prominent growth lines present and extending posteriorward across ramp. Base demarcated by low angulation. Ornament on base consisting of many closely spaced unbeaded spiral ribs, anteriorward becoming broader and beaded toward umbilicus and producing cancellate ornament. Aperture subcircular. Outer and inner lips thin. Peristome discontinuous. Umbilicus wide, its rim angulate and demarcated by moderately strong and beaded spiral rib. Umbilical wall with stronger cancellate ornament than area immediately posterior to umbilical rim. Growth lines prosocline, tilted 28° from vertical.

Holotype: LACMIP 13682, height 8.7 mm, diameter 9.4 mm.

Paratype: LACMIP 13683, LACMIP loc. 22900.

Type Locality: LACMIP 22900, Bald Hills, Ono area, Shasta County, northern California (Area 3).

Geologic Age: Early late Albian (upper *Oxytropidoceras packardi* ammonite zone).

Distribution: Budden Canyon Formation, Chickabally Mudstone Member, Bald Hills, vicinity of Ono, Shasta County, northern California (Area 3); reworked Albian fossils in lower Turonian Venado Sandstone just south of Sites, Colusa County, northern California (Area 5).

Etymology: Named for Steffen Kiel who has made significant contributions to the study of Cretaceous vetigastropods.

Remarks: The examined material consisted of six specimens: five from loc. 22900 (type locality) and one from loc. 24369. Preservation is generally good. *Igonoia kieli* co-occurs with *I. shastana* new species at locs. 22900 and 24369. Locality 22900 is from the upper part of the Chickabally Mudstone Member, and Murphy (1956: figs. 3–5) plotted this locality (as loc. 2900) on his columnar section and on his geologic maps. On his figure 6, he plotted this locality near the top of the *Oxytropidoceras packardi* ammonite zone, and on the biostratigraphic chart shown by Murphy et al. (1969: fig. 2), it appears that this part of the zone is early late Albian in age.

The single specimen of *I. kieli* from loc. 24369 is from the Venado Sandstone. This member is of early Turonian age and contains reworked Albian fossils (Squires and Saul, 2004).

Igonoia kieli differs from *I. shastana* by slightly larger size, subsutural rib, much less uniform ornament, and obsolete ornament on the sides of the whorls. *Igonola kieli* is similar to *I. muiri* new species, but *I. kieli* differs by having larger size, subsutural rib much weaker on spire whorls, absence of flat ramp, less angulate shoulder, more spiral ribs on shoulder, and much less prominent growth lines incising the spiral ribs on the shoulder.

***Igonoia shastana* new species**
(Figures 9–16)

Diagnosis: Small-sized *Igonoia*, spiral ribs numerous and uniformly noded except on anterior half of last whorl and on posterior part of base of last whorl.

Description: Shell size small (up to height 7 mm, diameter 8.5 mm, same specimen). Shell height approximately 92% of shell diameter. Trochiform. Phaneromphalous. Spire moderately elevated, approximately 50% of shell height. Pleural angle approximately 84°. Protoconch most likely less than one whorl. Teleoconch approximately 4.5 whorls. Suture impressed. All whorls with rounded sides. Ornament obsolete on two earliest whorls. Ornament on remaining whorls consisting of many closely spaced spiral ribs, beaded except on anterior half of last whorl and on posterior part of base of last whorl. Base demarcated by low angulation. Spiral ribs on base anteriorward becoming wider and bearing beads that become elongate near umbilical rim. Aperture circular. Outer and inner lips thin. Peristome probably discontinuous. Umbilicus wide, its rim angulate and demarcated by spiral rib wider and more strongly beaded than adjacent spiral ribs on base. Umbilical wall cancellate. Area abaxial to umbilical rim with irregularly spaced incised growth lines. Growth lines prosocline, tilted approximately 35° from vertical.

Holotype: LACMIP 13684, height 6.3 mm, diameter 6.2 mm.

Paratype: LACMIP 13685, LACMIP loc. 24369.

Type Locality: LACMIP 28757, Thompson Canyon, Yolo County, northern California (Area 6).

Geologic Age: Early late Albian (upper *Oxytropidoceras packardi* ammonite zone).

Distribution: Budden Canyon Formation, upper Chickabally Mudstone Member, Bald Hills, Ono area, Shasta County, northern California (Area 3); reworked Albian fossils in upper Cenomanian "Antelope" shale (upper part), just south of Sites, Colusa County, northern California (Area 5); and reworked Albian fossils in Turonian Venado Sandstone, Thompson Canyon, north

of Putah Creek, Monticello Dam area, Yolo County, northern California (Area 6).

Etymology: Named for its occurrence in Shasta County, northern California.

Remarks: The examined material consisted of eight specimens: three from USGS loc. M-177 (see Squires and Saul [2004: 500] for locality details); two from LACMIP loc. 22900; two from 24369; and one from 28757 (type locality). Distinction between the protoconch and earliest teleoconch whorl cannot be made because the shell is missing in these areas.

Igonoia shastana co-occurs with *I. kieli* new species at locality 22900 in the upper part of the Chickabally Mudstone Member, and both co-occur as reworked Albian material at loc. 24369 in the Venado Sandstone. The USGS loc. M-177 specimens also represent reworked material but are from the upper part of the "Antelope" shale in beds approximately 23 to 30 m below the base of the overlying Venado Sandstone.

According to the LACMIP records, loc. 28757 is in the Yolo Formation. On Matsumoto's (1960: fig. 9) map, this locality plots near the contact between this formation and the underlying Venado Sandstone. Locality 28757 is most likely located in the Venado Sandstone, thus the specimens are also reworked material.

Igonoia shastana and *I. kieli* are somewhat similar in that their early whorls are smooth and a portion of their last whorl has either diminished or obsolete ornament. *Igonoia shastana* differs from *I. kieli* by slightly smaller size, absence of a subsutural rib, mch more uniform ornament, and ornament on the sides of the whorls. No known specimens show intermediate morphology between the two species. Future collecting might reveal such specimens, and, hence, the two species could be shown to be conspecific.

***Igonoia onoensis* new species**
(Figures 17–23)

Sollariella stewarti Murphy and Rodda, 1960: 839 (in part).

Diagnosis: Small-sized *Igonoia*, ramp rounded and covered by four to five spiral ribs bearing prominent beads arranged in rows, whorl sides with weak and unbeaded spiral ribs, and basal ornament strong, including wide umbilical cord.

Description: Shell size small (up to height 7 mm, diameter 7 mm, same specimen), glossy surface. Shell height approximately same as shell diameter. Trochiform. Phaneromphalous. Spire moderately elevated, approximately 56% of shell height. Pleural angle 92°. Protoconch smooth (most likely less than one whorl), transition to teleoconch unclear; first half whorl of shell measures 0.38 mm (380 μm) diameter. Teleoconch approximately five whorls. Earliest teleoconch whorl with two equal-strength spiral threads (one on shoulder and one just anterior to shoulder) and three to four much weaker spiral threads; after another 180°, weaker spiral ribs disappear but spiral threads (two) on or near shoulder continue and become incipiently beaded. All teleoconch whorls with rounded sides. Suture impressed. Ramp rounded, narrow, and covered by four to five equant spiral ribs bearing prominent elongate beads arranged in rows. Ornament on whorl sides consisting of weak (rarely obsolete) unbeaded spiral ribs. Aperture subcircular. Outer and inner lips thin. Peristome probably discontinuous. Base ornamented with several strong, moderately narrow spiral ribs. Umbilicus wide, its rim angulate and demarcated by nodulose wide spiral rib. Area abaxial to umbilical rim with irregularly spaced incised growth lines. Growth lines prosocline, tilted 35° from vertical.

Holotype: LACMIP 13686, height 7.2 mm, diameter 7.2 mm.

Paratype: LACMIP 13687, LACMIP loc. 23476.

Type Locality: LACMIP 23476, Bald Hills, Shasta County, northern California (Area 3).

Geologic Age: Late Cenomanian (slightly older than *Igonoia stewarti*).

Distribution: Budden Canyon Formation, Bald Hills Member, Bald Hills, Ono area, Shasta County, northern California (Area 3).

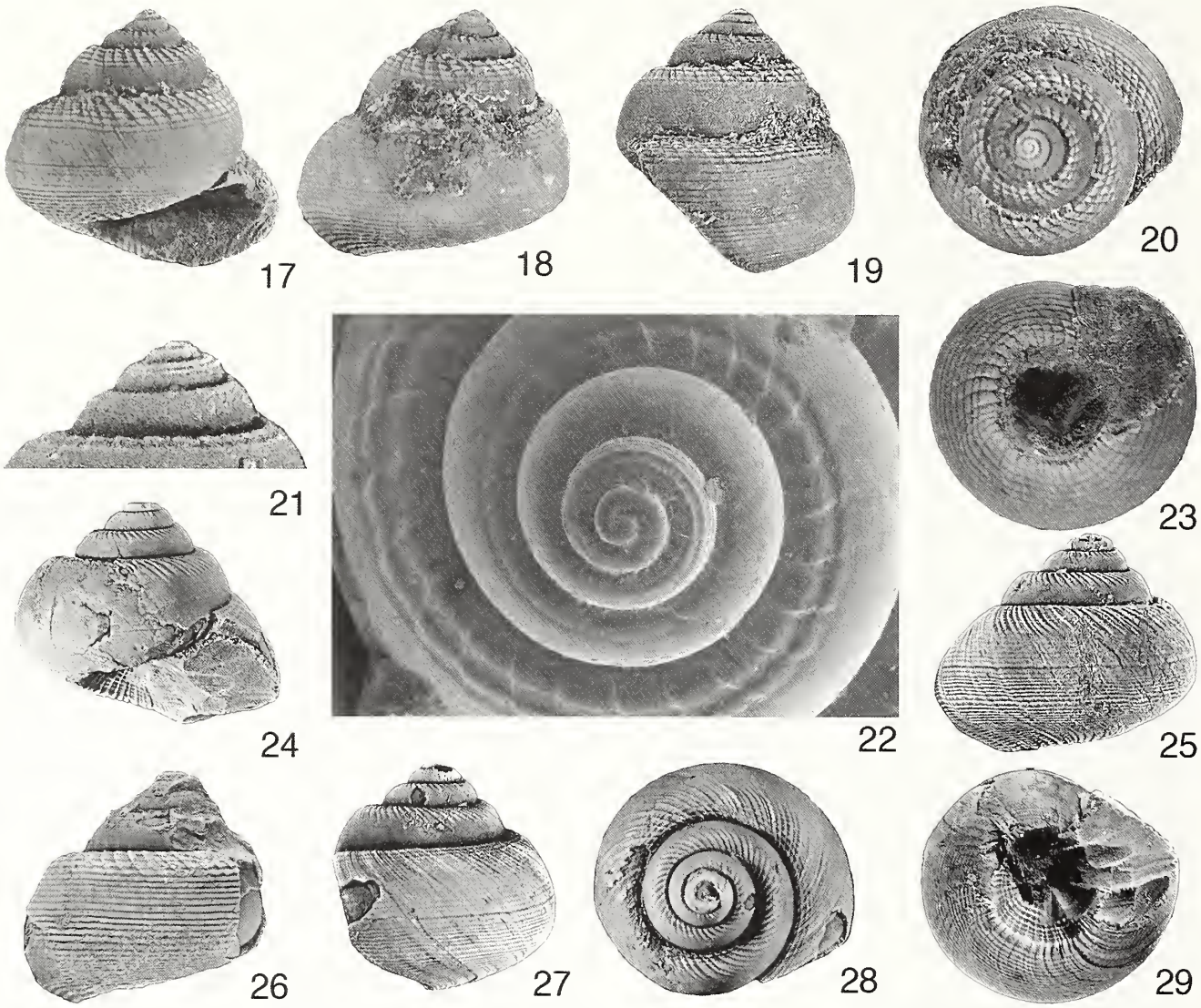
Etymology: Named for the town of Ono, Shasta County, California.

Remarks: Examined material consisted of four specimens (one early? adult and three juveniles), all from LACMIP loc. 23476 in the middle part of the Bald Hills Formation. One of the juveniles has its protoconch intact (Figures 21–22). Murphy and Rodda (1960) did not recognize that the specimens they identified as *S. stewarti* from LACMIP loc. 23476 represent a different species than *S. stewarti*. Although both species occur in the Bald Hills Member, *S. onoensis* is found slightly downsection from *S. stewarti*.

Murphy and Rodda (1960: fig. 2) reported that the aporrhaid gastropod *Arrhoges* (*Latiala*) *californicus* (Gabb, 1864) occurs at LACMIP loc. 23476. Popenoe (1983) assigned this aporrhaid a Cenomanian? to early Turonian age.

The new species is similar to *Igonoia stewarti* but *I. onoensis* is characterized by having prominently beaded spiral ornament, whereas *I. stewarti* is characterized by having weaker ornament consisting of raised growth lines. In addition, *I. onoensis* differs by having smaller size, more sloped ramp, beaded spiral ribs on the ramp, nearly obsolete spiral ribs on sides of the whorls, and slightly stronger ornament on the base.

The new species most resembles *Igonoia muiri* new species but differs by having a larger size, no subsutural cord, rounded shoulder (rather than angulate), and shoulder demarcated by several equal-strength spiral ribs, rather than by only two spirals, with the posteriormost



Figures 17–29. Cenomanian species of *Igonoia* new genus. Specimens coated with ammonium chloride. **17–23**. *Igonoia onoensis* new species. **17, 18, 19, 20, 23**. Holotype LACMIP 13686, LACMIP loc. 23476, height 7.2 mm, diameter 7.2 mm. **21–22**. Paratype LACMIP 13687, LACMIP loc. 23476, height 3 mm, diameter 4.5 mm. **21**. Abapertural view of spire tip. **22**. SEM image of left-lateral view of protoconch and early teleoconch whorls, width of view 2.5 mm. **24–29**. *Igonoia stewarti* (Murphy and Rodda, 1960). **24, 25, 27, 28, 29**. Holotype LACMIP 9821, LACMIP loc. 23763, height 8 mm, diameter 8.9 mm. **26**. Hypotype LACMIP 13688, LACMIP loc. 23465, height 6.2 mm, diameter 6.9 mm.

the strongest. In addition, on *I. onoensis*, the ornament on the base is not as weak abaxially.

***Igonoia stewarti* (Murphy and Rodda, 1960) new combination**
(Figures 24–29)

Solariella stewarti Murphy and Rodda, 1960: 839 (in part), pl. 103, figs. 4–5.

Diagnosis: Small-sized *Igonoia* with spire low, shoulder rounded with numerous very fine to fine spiral ribs crossed by prominently raised growth lines, basal ornament weak, and umbilical cord moderately strong.

Description: Shell size small (up to height 8 mm, diameter 9.2 mm, same specimen), glossy surface. Shell height approximately 89% of shell diameter. Trochiform. Phaneromphalous. Spire low, approximately 45% of shell height. Pleural angle 92°. Protoconch unknown. Teleoconch approximately six whorls, all with rounded sides. Suture nearly canaliculated. Shoulder rounded with three to five spiral ribs (noded), commonly very weak to weak. Spiral ornament elsewhere (on sides of whorls) consisting of numerous and closely spaced, weak to rarely moderately strong spiral riblets with tendency to being faint to obsolete. Shoulder with numerous and closely spaced, weak to moderately strong ribs coincident with

prominently raised growth lines. Aperture subcircular. Outer and inner lips thin. Peristome probably discontinuous. Base ornamented by numerous, very weak spiral riblets. Umbilicus rim angulate and demarcated by somewhat nodulose, moderately strong to strong spiral rib. Area just posterior to umbilical rim with irregularly spaced ribs. Area just abaxial to umbilical rim cancellate on some specimens. Umbilical wall cancellate. Growth lines prosocline, tilted 35° from vertical.

Holotype: LACMIP 9821 [= UCLA 28622], height 8 mm, diameter 8.9 mm.

Paratype: LACMIP 9822 (unfigured here) [= UCLA 28683], LACMIP loc. 23763.

Type Locality: LACMIP 23763, Bald Hills, Shasta County, northern California (Area 3).

Geologic Age: Late Cenomanian (slightly younger than *I. onoensis*).

Distribution: Budden Canyon Formation, Bald Hills Member, Bald Hills, Ono area, Shasta County, northern California (Area 3).

Remarks: The examined material consisted of nine specimens: four from LACMIP loc. 23464, three from LACMIP loc. 23465, and five from LACMIP loc. 23763. Preservation is good. Two of the specimens from LACMIP locality 23465 have stronger spiral ribs than normal for this species, and one of these specimens is illustrated in Figure 26. These variants were not mentioned by Murphy and Rodda (1960).

Murphy and Rodda (1960: 839) believed that *S. stewarti* is represented by some of the type material of *Igonoia angulata*. During this present investigation, this latter material was studied and found to consist of two species: *I. angulata* (Gabb) and *I. muiri* new species. The latter species does resemble *I. stewarti* (see *I. muiri* for a comparison).

Murphy and Rodda (1960) did not recognize that the specimens they identified as *Solariella stewarti* from LACMIP loc. 23476 represent a different species. In this present report, these specimens are identified as *Igonoia onoensis* new species, which is found in the middle part of the Bald Hills Member of the Budden Canyon Formation.

Igonoia stewarti is present in the upper half of the Bald Hills Member of the Budden Canyon Formation (Murphy and Rodda, 1960: 839, text-fig. 2). The associated macrofauna, especially the species of the gastropods *Gyrodes greeni* Murphy and Rodda, 1960 and *Gyrodes allisoni* Murphy and Rodda, 1960, are indicative of a late Cenomanian age (Popenoe et al., 1987: fig. 1). Murphy and Rodda (1960: fig. 2) also reported that the ammonite *Desmoceras* (*Pseudouhligella*) cf. *barryae* was found with *S. stewarti* at LACMIP loc. 23464, and Matsumoto (1959: 7) reported that this ammonite "seems to occur in the Cenomanian." Murphy and Rodda (1960) reported the ammonite *Turrilites dilleri* from loc. 23464. Rodda (1959) assigned this ammonite a Cenomanian age. Murphy and Rodda (1960) also reported that *S. stewarti* is also present in the "formation" that overlies the Bald Hills "formation." Using the revised stratigraphy of Murphy et al. (1969), this overlying "formation" is the Gas Point Member (Cenomanian to Turonian) of the Budden Canyon Formation. The present author, however, was unable to confirm a Gas Point Member occurrence of *I. stewarti*.

***Igonoia vacca* new species**
(Figures 30–34)

Diagnosis: Small-sized *Igonoia* with spire low and teleoconch bearing widely spaced, narrow spiral ribs crossed by widely spaced and raised growth lines, especially on rounded shoulder.

Description: Shell size small (up to height 7 mm, diameter 8 mm, same specimen). Shell height slightly less or approximately same size as shell diameter. Trochiform. Phaneromphalous. Spire low, approximately 46% of shell height. Pleural angle 85°. Protoconch unknown. Teleoconch approximately six convex whorls. Suture impressed; sutural area flattish on penultimate whorl. Teleoconch approximately four convex whorls. Shoulder area rounded. Ornament consisting of widely spaced, narrow spiral ribs; spire whorls with five riblets; spiral ribs on last whorl somewhat clustered together: two near suture, one on shoulder, four to five on sides of whorls, and numerous ones on base. Spiral ribs on base gradually become slightly stronger near umbilical rim where raised growth lines cross spiral ornament. Aperture circular. Outer and inner lips thin. Peristome discontinuous. Umbilicus moderately wide, its rim angulate and demarcated by beaded spiral cord with beads grading into nodes toward anterior end of columella. Umbilical wall cancellate. Growth lines prosocline, tilted 30° from vertical.

Holotype: LACMIP 13689, height 5.6 mm, diameter 6.6 mm.

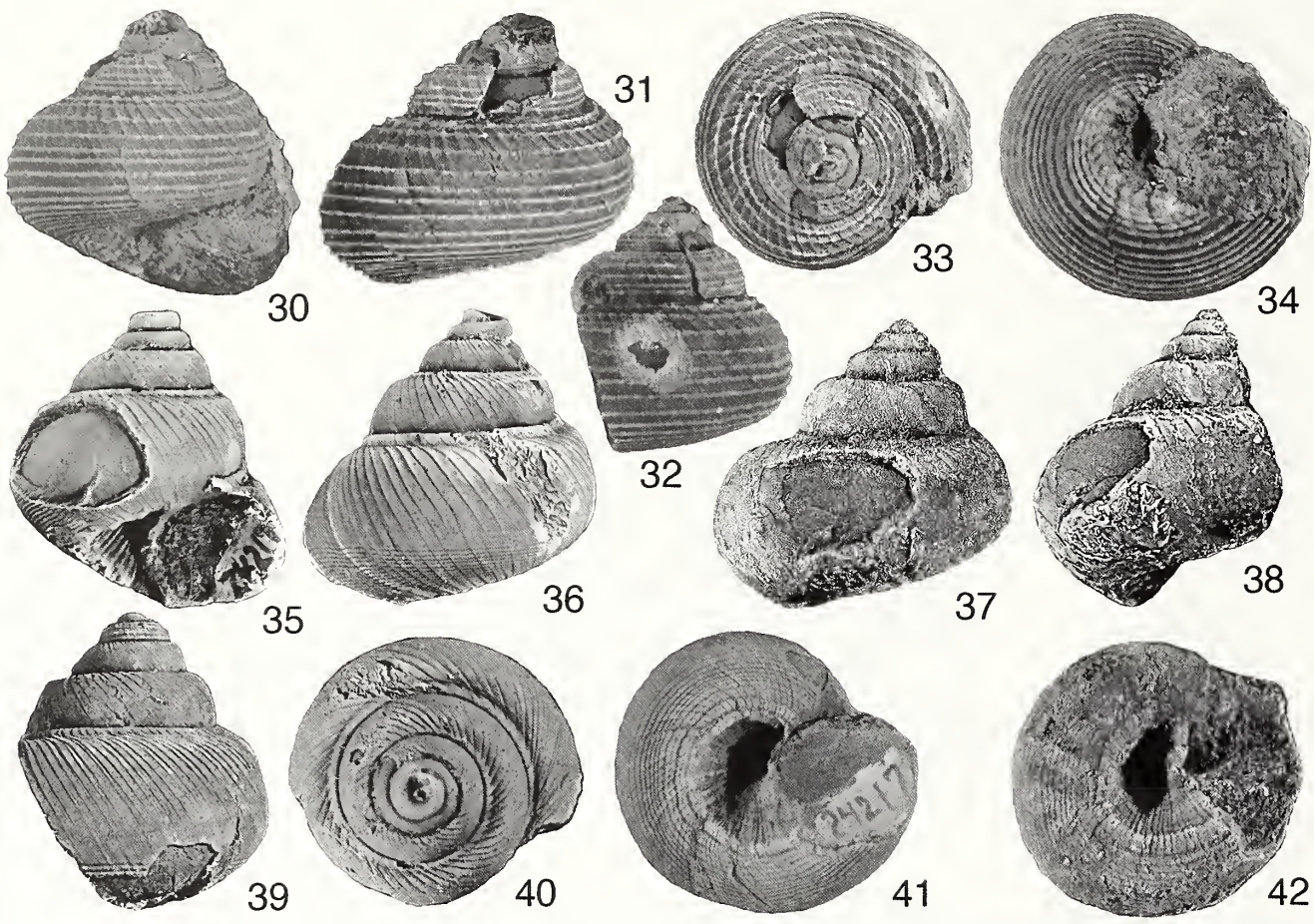
Type Locality: LACMIP 25421, east of Redding, Shasta County, northern California (Area 2).

Geologic Age: Late Turonian.

Distribution: Redding Formation, Melton Sandstone Member, east of Redding, Shasta County, northern California (Area 2); Ladd Formation, Baker Canyon Member, Santa Ana Mountains, Orange County, southern California (Area 8).

Etymology: Named for its occurrence in the Cow Creek area east of Redding, Shasta County, northern California; *vacca*, Latin, meaning cow, used as a noun in apposition.

Remarks: The examined material consisted of 17 specimens, and nearly all of them are from the Redding



Figures 30–41. Late Turonian and late Santonian species of *Igonoia* new genus. Specimens coated with ammonium chloride. **30–34.** Late Turonian *Igonoia vacca* new species, holotype LACMIP 13689, LACMIP loc. 25421, height 5.6 mm, diameter 5.6 mm. **35–42.** Late Santonian *Igonoia occidentalis* (Whiteaves, 1903). All specimens coated with ammonium chloride. **35, 36, 40.** Hypotype LACMIP 13690, LACMIP loc. 24217, height 8.7 mm, diameter 7 mm. **37–38.** Paratype GSC 5918a, Nanaimo area, Vancouver Island, British Columbia, height 5.5 mm, diameter 7.1 mm. **38.** Left-lateral view. **39.** Hypotype LACMIP 13691, LACMIP loc. 10794, height 7 mm, diameter 6.6 mm. **41.** Hypotype LACMIP 13692, LACMIP loc. 24217, diameter 10 mm. **42.** Paratype GSC 5919, Nanaimo area, Vancouver Island, British Columbia, diameter 6.9 mm, x5.4.

Formation. Most of the specimens have good preservation. The new species somewhat resembles *Igonoia shastana* new species, but the former differs by having non-beaded spiral ribs and narrower and much more widely spaced ribs.

Igonoia occidentalis (Whiteaves, 1903) new combination

(Figures 35–42)

Solariella (*radiatula* ? var.) *occidentalis* Whiteaves, 1903: 368–369, pl. 45, figs. 5, 5a.
Solariella roddai Saul, 1959.

Diagnosis: Moderately small-sized *Igonoia* with shell height greater than shell diameter, commonly with prominent subsutural cord, and raised growth lines stronger than nearly obsolete spiral ribs, except on base, on subsutural spiral cord, and on umbilical rim.

Description: Shell size moderately small (up to height 13 mm (estimated), diameter 12 mm, same specimen). Shell height approximately 15% greater than shell diameter. Trochiform. Phaneromphalous. Spire moderately high, approximately 59% of shell height. Pleural angle approximately 81°. Protoconch unknown. Teleoconch approximately five to six whorls, all with rounded sides. Suture impressed, rimed by prominent, unnoded subsutural cord. Shoulder narrow. Ornament generally weak and crossed by raised growth lines. Upper spire whorls with cancellate ornament. Lower spire whorls with many wide-spaced, flat ribs separated by finely incised lines. Last whorl similar to lower spire whorls, except for base with many weak and closely spaced spiral ribs that become slightly stronger anteriorward. Aperture circular. Outer lip thin, inner lip thicker and projecting slightly out over umbilicus. Peristome discontinuous. Umbilicus moderately wide, its rim angulate and demarcated by spiral rib, weakly beaded with beads

decreasing in strength anteriorward. Base of last whorl near umbilical rim and umbilical wall cancellate. Growth lines prosocline, tilted 30° from vertical.

Holotype: GSC 5918, height 4.7 mm, diameter 6.9 mm.

Paratypes: GSC 5918a, 5918b, 5919, 5919a, all from the type locality.

Type Locality: Vicinity of Nanaimo, Vancouver Island, British Columbia (Area 1).

Geologic Age: Santonian.

Distribution: LOWER SANTONIAN: Haslam Formation, Benson Creek and Nanaimo River, both in the vicinity of Nanaimo, Vancouver Island, British Columbia (Area 1); Redding Formation, upper Member V, Clover Creek, east of Redding, Shasta County, northern California (Area 2). UPPER SANTONIAN: Redding Formation, Member VI, Clover Creek, east of Redding, Shasta County, northern California (Area 2); tentative occurrence in Chico Formation, top of Musty Buck Member, Chico Creek, Butte County, northern California (Area 4).

Remarks: Examined material consisted of 212 specimens, which represents justs over 80% of the known studied specimens of *Igonoia*. Preservation is moderately good. Whiteaves (1903) reported that some of his type material was collected (by others) from Brennan Creek in the vicinity of Nanaimo, Vancouver Island. According to R. Graham (person. commun.), it should read Benson Creek. *Igonoia occidentalis* is most abundant in lower Santonian rocks at LACMIP loc. 24246 (Area 2), where 168 specimens have been collected. A few weathered specimens tentatively identified as this new species are from the top of the Musty Buck Member in the Chico Formation, Butte County, northern California.

Igonoia occidentalis is similar to *Igonoia angulata* but differs from the latter by much larger shell size, suture not canaliculate, presence of subsutural rib, and raised growth lines extending from suture to suture on spire whorls and from suture to umbilical rim on last whorl. *Igonoia occidentalis* resembles the Upper Cretaceous margaritine *Atira ornatissima* (Gabb, 1864) from California but differs from the latter by having shell height greater than shell diameter, subsutural cord, non-sloping ramp, more prominent growth lines, inner lip not projected over edge of umbilicus, and umbilical rim demarcated by an angulation rather than a prominent spiral rib.

Stoliczka (1867–1868) reported *Solariella radiatula* Forbes, 1846, from southern India at the locale of Odiyam [= Odium of old usage], which, according to Sundaram et al. (2001), is stratigraphically situated in the upper Albian to Cenomanian Karai Formation. Although Whiteaves (1903) questionably identified *I. occidentalis* as *Solariella* (*radiatula* ? var.) *occidentalis*, this species is here identified as *I. occidentalis* because it is not Forbes's species *radiatula*.

***Igonoia angulata* (Gabb, 1869) new combination**
(Figures 43–47)

Margaritella angulata Gabb, 1869: 172 [in part], pl. 28, figs. 55.
Solariella angulata (Gabb). Stewart, 1927: 317, pl. 24, fig. 17.

Diagnosis: Very small-sized *Igonoia* with suture canaliculate, ornament prominent only on shoulder, prominently raised growth lines on periphery and on base of last whorl.

Description: Shell size very small (up to height 4.5 mm (estimated), diameter 4.8 mm, same specimen). Shell height approximately same as shell diameter. Trochiform. Phaneromphalous. Spire moderately high, approximately 54% of shell height. Pleural angle 80°. Protoconch unknown. Teleoconch approximately four whorls. Suture canaliculate. All whorls with flattish sides. Shoulder angulate, crossed by many prominently raised growth lines that become obsolete near middle portion of whorls. Spiral ornament obsolete on spire whorls; spiral ornament on last whorl consisting of many very fine threads starting at middle portion of whorls and continuing onto base. Base demarcated by rounded angulation; base covered by many very fine spiral threads that become microscopically beaded anteriorward. Aperture elliptical. Outer and inner lips thin. Peristome probably discontinuous. Umbilicus rim angulate and demarcated by beaded spiral ribs. Growth lines prosocline, tilted approximately 33° from vertical.

Lectotype: ANSP 4238 (designated by Stewart (1927) but missing since 1992 (P. Colloman, person. commun.), height 4.4 mm, diameter 5 mm.

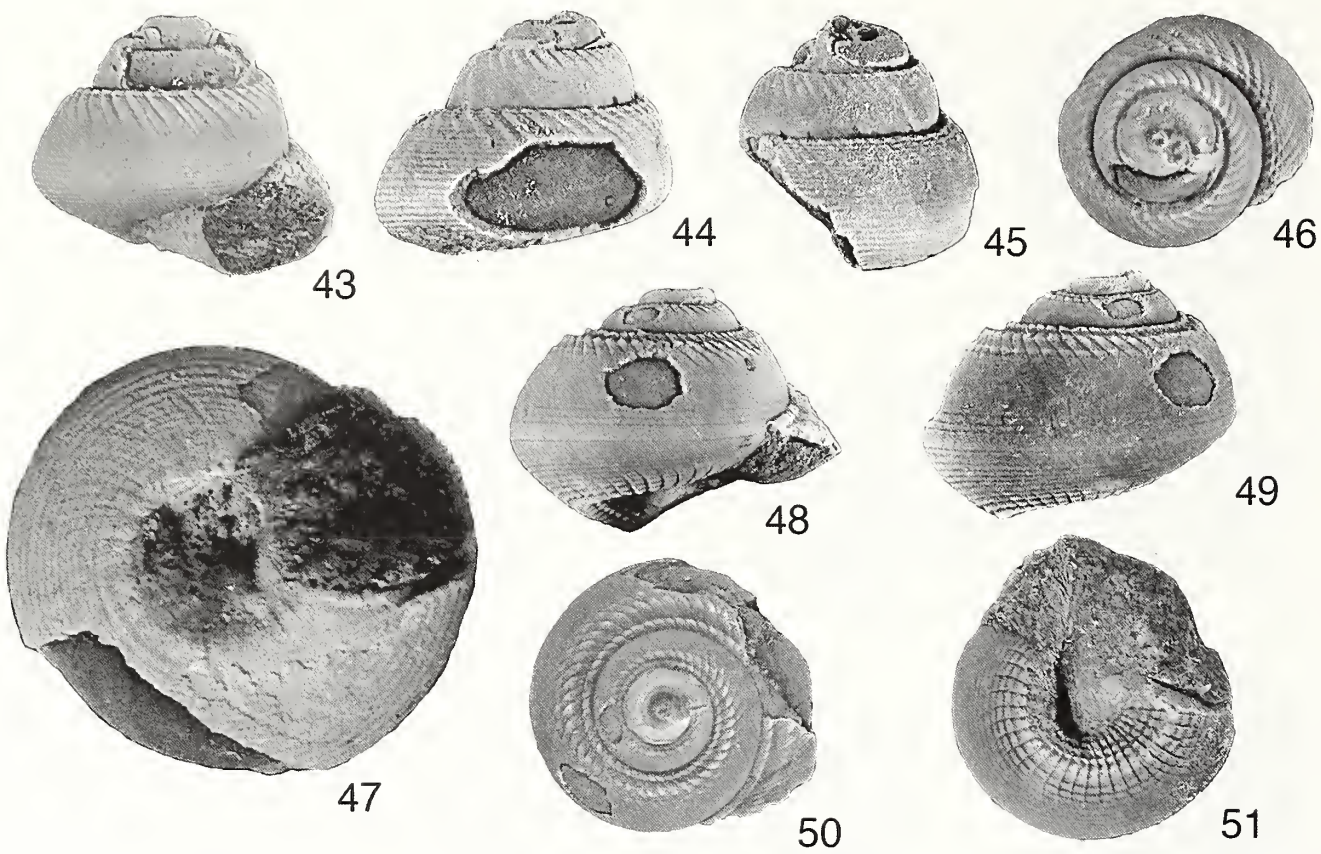
Paralectotypes: ANSP 79512 [ex-ANSP 4238].

Type Locality: LACMIP 23312, Franklin County, near Martinez, Contra Costa County, northern California (Area 7).

Geologic Age: "Mid" Maastrichtian (late early to middle late).

Distribution: Panoche Formation, Franklin Canyon, southwest side of Martinez, Contra Costa County, northern California (Area 7).

Remarks: The examined material consisted of two specimens, both previously part of a supposed group of six ANSP paralectotypes of *Solariella angulata*. Five of these specimens are stored together as ANSP 79512 [ex 4238] and the sixth one is ANSP 79153. Of the five ANSP 79512 specimens, only two are like the drawing provided by Gabb (1869) and the photograph provided by Stewart (1927) of the lectotype of *S. angulata*. Of the remaining three specimens, two belong to *Igonoia muiri* new species, and one is an indeterminate species because it has lost most of its shell. The ANSP 79153 specimen is a badly crushed naticid? gastropod, and the



Figures 43–51. Maastrichtian species of *Igonoia* new genus. **43–47.** *Igonoia angulata* (Gabb, 1869), paralectoype ANSP 79512 [*ex* 4238], LACMIP loc. 23312, height 4.4 mm, diameter 5 mm. **48–51.** *Igonoia muiri* new species, holotype ANSP 81350, LACMIP loc. 23312, height 5.2 mm, diameter 7 mm.

rock matrix filling its aperture is light in color, soft, and totally unlike the blackish-gray, well-cemented siltstone in the apertures of the two specimens of *I. angulata* and the two specimens of *I. muiri*.

Gabb (1869) reported that the type locality of his *S. angulata* to be "at Martinez." He did not collect the type specimens; they were sent to him by a eollector. The area immediately surrounding this eity has stratigraphie units ranging in age from Late Cretaeeous to Miocene, and there are several faults (Weaver, 1953). The location of the type locality of *I. angulata*, therefore, has been poorly known; subsequently, the geologic age of this species has been uncertain. Inspection (by the present author) of the rock type associated with the two speeimens of *I. angulata* revealed a match with the roek type associated with the gastropod *Atira inornata* (Gabb, 1864), which is also found at LACMIP loc. 23312. Squires (2010) reported that *A. inornata* is of "mid" Maastrichtian age. According to the LACMIP records, this locality is the same as Gabb's original "at Martinez" Cretaceous locality. On Dibblee's (1980) geologic map of the area, this locality plots in the Panoche Formation.

Cossmann (1918: 257) based the earliest record of genus *Periaulax* Cossmann, 1888, on "*Margaritella*" *angulata* Gabb, 1869 from the so-called "Chico Group" at Martinez, California. He assigned these strata to the "Aturian," whieh aeeording to Harland et al. (1982: 110), generally refers to the Campanian.

Igonoia muiri new species
(Figures 48–51)

Margaritella angulata Gabb, 1869: 172 [in part].
Solariella angulata (Gabb). Stewart, 1927: 317 [in part].

Diagnosis: Very small-sized *Igonoia* with spire low, beaded subsutural rib, ramp flat, shoulder angulate and bearing two spiral ribs (beaded), subsutural area and ramp incised by prominently raised growth lines, and sides of whorls smooth.

Description: Shell size very small (up to height 5 mm (estimated), diameter 7 mm, same speeimen). Shell height approximately 90% of shell diameter. Trochiform. Phaneromphalous. Spire low, approximately 43% of shell height. Pleural angle approximately 95°. Protoeonch unknown. Teleoconeh approximately four whorls. Suture impressed, bordered by prominent subsubtural beaded rib. Ramp flat. Spire whorls with sides somewhat rounded; last whorl with sides flattish. Ornament on whorls eonsisting of beaded subsutural rib, stronger

beaded spiral rib on angulate shoulder, and one other spiral rib (weaker) just anterior to shoulder; all three ribs incised by moderately widely spaced prominently raised growth lines that become obsolete on middle portion of sides of whorls. Base demarcated by rounded angulation; several weak spiral threads posterior to angulation. Ornament on base consisting of many spiral ribs becoming stronger and beaded anteriorward; beads crossed by prominent growth lines, thereby producing cancellate ornament. Aperture elliptical. Outer and inner lips thin. Peristome discontinuous. Umbilicus wide, its rim angulate and demarcated by prominently beaded spiral rib. Umbilical wall cancellate. Growth lines prosocline, tilted 42° from vertical.

Holotype: ANSP 81350, height 5.2 mm, diameter 7 mm.

Paratype: ANSP 81351 (unfigured), from the type locality.

Type Locality: LACMIP 23312, Franklin County, near Martinez, Contra Costa County, northern California (Area 7).

Geologic Age: "Mid" Maastrichtian (late early to middle late).

Distribution: Panoche Formation, Franklin Canyon, southwest side of Martinez, Contra Costa County, northern California (Area 7).

Etymology: Named for John Muir, early Californian naturalist and visionary conservationalist, whose home is in the immediate vicinity of the type locality of the new species.

Remarks: The examined material consisted of two specimens, previously part of a supposed group of six paralectotypes of *Solariella angulata* (see "Remarks" for *I. angulata*).

The new species occurs with *I. angulata* at LACMIP loc. 23312, which occurs in strata of "mid" Maastrichtian age (see "Remarks" for *I. angulata*). The new species differs from *I. angulata* by larger size, wider shell, non-canaliculate suture, subsutural rib, two spiral (beaded) ribs on shoulder, and much stronger spiral ribs on base.

Igonoia muiri is most similar to *I. onoensis* new species but differs from the latter by having smaller size, subsutural cord, angulate shoulder (rather than rounded), shoulder demarcated by only two spirals, with the posteriormost the strongest (rather than with approximately seven spirals, all nearly equal in strength), ornament on base less well developed, and ornament on base somewhat obsolete near middle portion of sides of whorls.

PALEOGEOGRAPHIC AND PALEOCLIMATIC COMMENTS

Igonoia kieli and *I. shastana*, the earliest known representatives of this new genus, existed in the Albian, which, according to Hallam (1992: fig. 4.8) and Frakes (1999), was a time of warming ocean waters and a pronounced sea-level rise. During the Albian and Cenomanian, *Igonoia* reached its peak diversity (two species during each stage) in northern California. There was exceptional warming during the Turonian, as well as one of the highest sea-level stands of the entire Cretaceous (Haq et al., 1987; Frakes, 1999). These conditions would have been ideal for *I. vacca* to become widespread in the study area, but the number of specimens is low. In addition to being found in northern California (i.e., approximately 42° N) (Area 2), *I. vacca* also ranged as far south as the Santa Ana Mountains in southern California (Area 8). Based on an analysis of paleomagnetic studies (Dickerson and Butler, 1998: fig. 1), the Santa Ana Mountains are part of a microplate tectonic terrane that would have been even slightly farther south (approximately 32° N, compared to its present-day location at 33° N). Based on volutodermine and opine bivalve studies (Saul and Squires, 2008; Squires and Saul, 2009), warm-temperate surface waters were the norm for the study area and the approximate position of the Late Cretaceous subtropical/warm-temperate boundary shifted from 43° N in the Turonian to 36° N in the Campanian and Maastrichtian.

During the latest Turonian to Coniacian there was marked cooling (Frakes, 1999) and a drastic drop in sea level (Hallam, 1992). No Coniacian specimens of *Igonoia* are known. Relative to the Coniacian, there was some warming during the Santonian and early part of the Campanian (Frakes, 1999), and sea level remained generally high (Hallam, 1992). The time of greatest abundance of *Igonoia* specimens was the Santonian, with most of the specimens found in northern California. The occurrence of *I. occidentalis* in the Nanaimo Group on Vancouver Island, British Columbia (Area 1) is an artifact of tectonic transport. Work on Cretaceous mollusks by Squires and Saul (2006: 86) and Saul and Squires (2008: 214) supported the contention that the Nanaimo Group was deposited not any farther south than northern California.

No Campanian age specimens of *Igonoia* are known, and the only study area specimens of *Igonoia* Maastrichtian age are two specimens each of *I. angulata* and *I. muiri*.

In summary, the localities of *Igonoia* are mainly clustered around the 40° N latitude in northern California (Figure 1), thus they plot within the warm-temperate water regime (see Saul and Squires, 2008: fig. 3). Prior to tectonic transport complications, study area *Igonoia* were most widespread, but few in number, during the relatively warm time of the Turonian when temperate waters expanded latitudinally. The highest abundance of specimens, however, was during the Santonian,

which was a cooler time relative to the Turonian. The lack of Campanian-age *Igonoia* and the paucity of Maastrichtian-age specimens are very puzzling, and the reasons await further study.

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APPENDIX 1. TYPE LOCALITIES OF THE NEW SPECIES

Localities are LACMIP. All quadrangle maps listed below are U. S. Geological Survey maps.

Detailed information about the other cited localities in the text is available via the following: LACMIP website: <http://ip.nhm.org/ipdatabase/locality_show>; UCMP website: <http://ucmpdb.Berkeley.edu/loc.html>.

22893. Dark brown sandstone, 5260 ft. S 28.5° W of intersection of Ono-Igo Road and Cottonwood-Igo Road, on East Fork of Hulen Creek, Ono Quadrangle (15 minute), Bald Hills, Ono area, Shasta County, California. Budden Canyon Formation, Huling Sandstone Member. Age: Late Aptian. Collector: M. A. Murphy, January 1, 1951.

22900. 1500 ft. N18°W of confluence of North Fork of Cottonwood Creek and Huling Creek; on Huling Creek, in conglomeratic sandstone forming the narrows; is first sandstone below junction with east fork of Huling Creek, NE/4 of sec. 17, T. 30N, R. 6W, Ono Quadrangle (15-minute, 1952), Bald Hills area, Shasta County, California. Budden Canyon Formation, Chickabally Mudstone Member. Age: Early late Albian (upper part of *Oxytropidoceras packardi* ammonite zone). Collector: M. A. Murphy, January, 1953.

23312. Crest of 500 ft. ridge on N side of Franklin Canyon due W of the old John Muir place at S end of city of Martinez, northeastern corner of Briones Valley Quadrangle (7.5 minute, 1959), Contra Costa County, California (= Gabb's original Martinez Cretaceous locality). Great Valley Sequence. Age: "Mid" Maastrichtian (late early to middle late). Collector: W. P. Popenoe, August, 1944.

23476. Hard concretionary sandstone, 3000 ft. S of NW corner of sec. 30, T. 30 N, R. 6 W, Ono Quadrangle (15 minute), Coyote Creek, Bald Hills, Ono area, Shasta County, California. Budden Canyon Formation, Bald Hills Member. Age: Cenomanian. Collector: P. U. Rodda, August, 1955.

23896. Hard concretionary sandstone in gully bottom and on slope to the west, 570 ft. W and 2300 ft. S of NE corner of sec. 25, T. 31 N, R. 6 W, Redding Quadrangle (7.5 minute, 1957, photorevised 1969), Clear Creek area, Shasta County, northern California. Budden Canyon Formation, Chickabally Mudstone Member. Age: Late early Albian (*Brewericeras hulenense* ammonite zone). Collectors: P. U. Rodda, M. A. Murphy, and W. P. Popenoe, August, 1955.

24246. Sandstone bed 30–40 ft. stratigraphically above conglomerate at center of W line of sec. 33, on N side of divide between Clover and Basin Hollow creeks, Shasta County, northern California. Redding Formation, upper Member V. Age: Early Santonian. Collector: W. P. Popenoe, August 25, 1959.

25421. Sandstone nodules in shale, left bank of Little Cow Creek, about 5 ft. above the channel bottom, 75 m NE (upstream) from intersection of the creek bed with the line fence, S line of sec. 9, T. 32 N, R. 3 W., Millville Quadrangle (15-minute, 1953), Shasta County, California. Formation: Redding Formation, Melton Sandstone Member. Age: Late Turonian. Collector: W. P. Popenoe, summer 1937.

28757. 2700 ft. N of Putah Creek, section 20, T. 8 N, R. 2 W, Thompson Canyon, just NE of Monticello Dam (forming Lake Berryessa), near the letter "y" in the word "Canyon," Monticello Dam Quadrangle (7.5 minute, 1959), Yolo County, Venado Sandstone (containing reworked Albian fossils). Age: Turonian (see Matsumoto, 1960: 38).

Reproductive biology of *Octopus tehuelchus* d'Orbigny, 1834 (Cephalopoda: Octopodidae) in southern Brazil

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ABSTRACT

Octopus tehuelchus is a small octopus endemic to subtropical and temperate waters of the southwestern Atlantic continental shelf. Its reproductive biology was studied by examining 319 individuals, measuring 20 to 79 mm mantle length (ML), collected between 1979 and 2009 along the coast of southern Brazil. Females are more numerous in shallower waters and attain larger size than males. Fully mature males and females were observed in all seasons and mean mantle length at maturity was 46 mm for females and 27 mm for males. The number of intraovaric oocytes of maturing females ranged from 20 to 448 and was positively correlated with female size. In mature females, a wide range of intraovaric oocytes diameters was observed, in some cases with a bimodal distribution. The number of eggs in the four layings ranged from 86 to 237, the diameters ranged from 8.2 to 14.5 mm and no bimodality was observed. Digestive gland grew proportionally to body weight along maturation in females but not in males, suggesting accumulation of reserves for spawning and parental care in females and priority for sexual maturation over growth in males. The comparison of the reproductive cycle of *O. tehuelchus* in southern Brazil with populations from northern Patagonia shows that the species has the potential for year round spawning, but ecological constrains only allows it to express this potential in the lower latitudes of its distribution.

Additional keywords: Mollusca, Reproductive cycle, sexual maturation, fecundity, southwestern Atlantic

INTRODUCTION

Cephalopods have developed a wide array of reproductive strategies, which enable them to occupy all marine habitats (Rocha et al., 2001). Particularly, the family Octopodidae has experienced an intense speciation, occupying coastal benthic environments from the tropics to temperate regions (Norman, 2003). In this family, a range of reproductive strategies occurs, from species with wide distribution, large body size, small eggs, high fecundity and pelagic hatchlings, such as *Octopus vulgaris* (Guerra, 1975; Mangold, 1987; Rocha et al., 2001; Otero et al., 2007; Villanueva and Norman, 2008) to more narrowly distributed species, with small body size, larger eggs, low fecundity and benthic development, such as *Octopus tehuelchus* (Pujals, 1982; Iribarne, 1991; Ré, 1998). This last species occurs from subtropical southeastern Brazil (20° S) (Haimovici and Perez, 1991) to the temperate habitats of San Jorge Gulf, in northern Patagonia, Argentina (43°S) (Ré and Simes, 1992; Ré, 1998).

In southern Brazil, *Octopus tehuelchus* occurs over the continental shelf, as deep as 100 m depth and usually associated with gastropod shells (Haimovici and Andriguetto, 1986). Due its low abundance in commercial landings, its life cycle and biology are poorly known in Brazil. However, the species is frequently found in stomach contents of demersal teleosts and marine mammals from this region (Santos and Haimovici, 2002). In the Patagonian gulfs, the species is commercially exploited as small artisanal fishery (Storero, 2010).

Most information on the growth and reproductive biology of the species comes from studies conducted in Patagonia, in an environment predominantly that includes rocky bottoms, discharge of freshwater creeks and channels, high tidal range (up to 9 m), and large seasonal variation of temperature and luminosity (Pollero and Iribarne, 1988; Iribarne, 1991; Navarte et al., 2006; Klaich et al., 2008; Storero et al., 2010). This environment contrasts with that of southern Brazil, which presents sandy and muddy bottoms, small tidal range and, due to its more northerly distribution, temperature rarely below 12°C, even in the cold months (Haimovici et al., 1996) and lower variation in luminosity between winter and summer (Bakun and Parrish, 1990).

The aim of this work is to study the reproductive biology of *Octopus tehuelchus* in the subtropical environment of the continental shelf in southern Brazil, which will allow for a better understanding of the reproductive strategy along the species distribution.

MATERIALS AND METHODS

Data Collection: Specimens of *Octopus tehuelchus* were collected from bottom trawl surveys by the R/V

Atlântico Sul and from commercial trawling along southern Brazil in the 28° S to 34° S range at depth from 15 to 100 m, between 1979 and 2009. Specimens were fixed in 10% formalin and preserved in 70% ethanol.

All preserved individuals, 125 males and 194 females, had their total length (TL), dorsal mantle length (ML), total body weight (BW), and digestive gland weight (DGW) recorded. Females had their ovary weight (OW), oviducts weight (including the oviducal glands) (OvW), and maximum diameter of oviducal glands recorded. Maximum diameters of oocytes (MDO) were measured with a caliper to the nearest 0.1 mm. All developing intraovaric oocytes over 4 mm were counted. Four egg clutches were collected on gastropod shells, spawned eggs were measured and recently hatched individuals, without the yolk sac, were measured and weighed. In males, testis weight (TW) and spermatophoric sac (including the glandular system) weight (SSW) were weighed within 0.01 g precision. Spermatophores in the Needham's sac were counted and measured at the nearest 0.1 mm on a micrometric scale.

The reproductive cycle was analyzed by a combination of the monthly frequencies of males and females in each maturity stage and the monthly variations of the maturity and gonadosomatic indices.

A maturity index (MI) was calculated as MI = SSW/ (TW + SSW) for males and MI = OvW/ (OW + OvW) for females (Hayashi, 1970). The gonadosomatic index (GSI) was calculated as GSI = (SSW/ (BW – SSW)) × 100 for males and GSI = (OW/ (BW – OW)) × 100 for females (Otero et al., 2007). Digestive gland index (DGI) was calculated as DGI = (DGW/ (BW – DGW)) × 100, similar to the one used for *Octopus vulgaris* (Otero et al., 2007).

The maturity scale was modified from Guerra (1975), Pujals (1982), and Perez and Haimovici (1991). For females, five stages were defined based on the size, color and transparency of the oviducts and oviducal glands in preserved specimens as well as the mean diameter of the developing oocytes: *Immature (I):* translucent oviducts, oviducal glands little differentiated, with diameter usually smaller than 2 mm; *Initial maturity (II):* whitish oviducal glands between 2 and 3 mm in diameter and developing oocytes 2 to 4 mm long; *Intermediate maturity(III):* oviducal glands brown/black, 3 to 4.5 mm in diameter, most oocytes between 4 and 7.5 mm long; *Advanced maturity (IV):* enlarged oviducts, sometimes with oocytes being released, mean diameter of the larger oocytes over 7.5 mm; *Post-spawning (V):* ovary clearly flaccid with reduced size and few eggs in it, oviducts dilated and small oviducal glands.

The maturity scale for males included four stages: *Immature (I):* small and whitish testis, glandular system slightly differentiated and absence of spermatophores in the Needham's sac; *Initial maturity (II):* testis under development, usually heavier than the glandular system and Needham's sac with few (<20) spermatophores; *Advanced maturity (III):* testicle weight lighter than glandular system and Needham's sac full; *Post-liberation of spermatophores (IV):* glandular system still bulky, Needham's sac partially or totally empty, with spermatophores being released and testicle relatively small, striped and usually less heavy than the glandular system.

Potential fecundity was defined as the number of developing oocytes with diameters over 4 mm in ovaries of stages III and IV females. The few smaller ones, which were probably atresic, were discarded.

Data Analyses: Reproductive indices were compared with the non-parametric Kruskal-Wallis test for multiple comparisons, because assumptions for normality and homogeneity of variance were not satisfied.

The sex ratio was calculated for the categories "month", "mantle length", and "depth". To allow for comparable numbers of specimens, ML was grouped in four 15 mm classes and depth in three classes: under 30 m, from 30 to 59 m, and 60 m and over. Significant deviations from the 1:1 proportion were tested using the χ^2 test, adjusted to Yates correction (Zar, 1984).

Length-weight relationships were estimated for the total sample and according to sex. Data were adjusted to power model ($y = ax^b$), where y = BW; x = ML; a = the y-intercept; and b = the slope. The goodness of fit was expressed by r^2 and the analysis of covariance (ANCOVA) (Zar, 1984) was used to test for differences in the slope of log-transformed relationships.

The mean mantle length at maturity (ML50%) was estimated starting from the proportion (Pi) of stages III and IV individuals, grouped in 6 mm ML classes, adjusted to the logistic model: $Pi = 1–\{1/ 1 + \exp [– (\alpha + \beta MLi)]\}$

The Bhattacharya method (Bhattacharya, 1967; King, 2007) was used to discriminate normal components in the diameter frequency distribution of intraovaric oocytes.

RESULTS

Sex Ratio: Females were significantly more abundant that males (174:125), however the sex ratio did not differ significantly when grouped monthly (Table 1). The proportion of females was significantly higher among the specimens larger than 45 mm ML ($\chi^2 = 13.89$ and 5.18; $p < 0.05$) (Table 2), suggesting that females grow larger than males. The number of females was higher in all depth ranges, however, the differences between sexes was only significant at depths shallower than 30 m ($\chi^2 = 4.17$; ($p < 0.05$) (Table 3).

Length-Weight Relationships: Females *O. tehuelchus* ranged from 21 to 79 mm ML (mean 47.2) and from 8.3 to 228.5 g BW (mean 69.5) and males ranged from 20 to 76 mm ML (mean 42.6) and 4.7 to 125.1 g BW (mean 46.0). The dorsal mantle length/total body weight relationships (ML/BW) were calculated only for individuals caught in 2009 (n = 64), which were less affected by the dehydration observed in specimens preserved in alcohol for long periods. Relationships were best described by the power equations (Table 4): females: BW = 0.0211 ×

Table 1. Monthly variation in sex ratio of *Octopus tehuelchus* in southern Brazil.

Month	Number	Females	Males	χ^2
Jan	49	59%	41%	1.67
Mar	5	40%	60%	0.40
Apr	14	50%	50%	0.07
May	18	67%	33%	2.00
Jun	43	51%	49%	0.05
Aug	14	64%	36%	1.21
Sep	44	64%	36%	3.30
Oct	14	57%	43%	0.36
Nov	56	63%	38%	3.52
Dee	30	40%	60%	1.23

Table 2. Sex ratio variation of *Octopus tehuelchus* aecording to ML 15 mm elasses in southern Brazil (*significant χ^2 departures from the 1:1 sex ratio $p < 0.05$).

ML Classes range (mm)	Number	Females	Males	χ^2
15 – 29.9	17	35%	65%	1.53
30 – 44.9	140	51%	49%	0.04
45 – 59.9	104	68%	32%	13.89*
> 60	38	68%	32%	5.18*

Table 3. Sex ratio variation of *Octopus tehuelchus* aecording to 30 m depth elasses in southern Brazil (*signifieant χ^2 departures from the 1:1 sex ratio $p < 0.05$).

Depth range (m)	Number	Mean females ML (mm)	Females	Males	χ^2
< 30	24	45	71%	29%	4.21*
30 – 59	171	45,0	56%	44%	2.58
> 60	58	47,8	60%	40%	2.50

$ML^{2.2098}$, males: $BW = 0.0113 \times ML^{2.3337}$ and both sexes combined: $BW = 0.0072 \times ML^{2.4772}$. Slope comparisons did not show heterogeneity between sexes (ANCOVA, $p = 0.634$). However, these results should be considered with care due to the low number of individuals, particularly of males (Table 4).

Maturation and Size-at-Maturity: Fully mature males and females were observed in all seasons. Therefore, the mean size and weight at maturity were calculated including specimens collected year round.

Females in stages I and II (n = 76) were observed in all size ranges including seven females over 60 mm ML (Figure 1). Females in stages III and IV (n = 95) measured over 24 mm ML and weighed over 30 g. Despite the small variation, the mean ML increased significantly with maturation ($p < 0.05$) (Table 5). The maturity curve of females showed a good fit to the logistic model ($r^2 = 0.980$) and $ML_{50\%}$ calculated was 45.9 mm (Figure 2).

Males in stages I and II (n = 58) were observed in all sizes including five individuals over 60 mm (Figure 1). All males in stages III and IV (n = 65) were over 30 mm ML and 15 g BW. The $ML_{50\%}$ was 27.4 mm, however, the maturity curve of males did not show a good fit to the logistic model ($r^2 = 0.129$) (Figure 2).

Seasonality: Females in stages I or II were observed in all months sampled. Stage III individuals were caught more frequently in April, June, and November and stage IV individuals were caught in all months sampled, mainly in January, August, and September (Figure 3). A single stage V female with an egg clutch was observed in July. Three other egg clutches without the spawned female were found in the same month and a fourth was observed in November. Reproductive indices were not homogeneous throughout all months ($p < 0.05$) (Fig 4). Higher (GSI) and lower (MI) associated to sexual maturity were observed in January (summer) and June, August, and September (late autumn to late winter).

Immature and initial maturity males (stages I and II) occurred year round, but more frequently in April, June and December. Stages III and IV also occurred in all sampled months, more frequently in January (summer), September, October, and November (late winter and early spring) (Figure 3). There were no significant differences in the monthly means of IM and GSI ($p > 0.05$), indicating mature males in all seasons (Figure 4).

In both sexes, maturity stages and reproductive indices support a year-round sexual maturation cycle.

Pre-spawning Oocytes and Spermatophores: The mean number of oocytes in the ovaries of 67 maturing females (stages III and IV) was 246.8 (range from 20 to 448). The diameter of the oocytes ranged from 1.8 to 13.9 mm (Table 5). A wide range of oocyte diameters was observed within the ovaries of every individual, in some cases with a bimodal distribution. The number of oocytes (ON) increased significantly with female ML ($ON = 1.4889 \times (ML)\ 1.3094$; $r = 0.524$ n=67) (Figure 5). Immature and initial maturity females (stages I and II, n = 68) had 185 oocytes in average (50 to 514), most with diameters under 4 mm (Table 5).

In stages III and IV males (n = 67), the number of stored spermatophores in Needham's sac ranged from 1

Table 4. Range of mantle length (ML) and total body weight (BW) and power regression parameters of length/weight relationships for females and males of *Octopus tehuelchus* caught in southern Brazil in 2009.

	n	min-max (mean) ML	min-max (mean) BW	A	B	r^2
Females	47	30–65 (49.9) mm	21.9–228.5 (123.4) g	0.0211	2.2098	0.7240
Males	17	28–52 (40.1) mm	32.5–119.4 (65.1) g	0.0113	2.3337	0.8290
Both sexes	64			0.0072	2.4772	0.8347

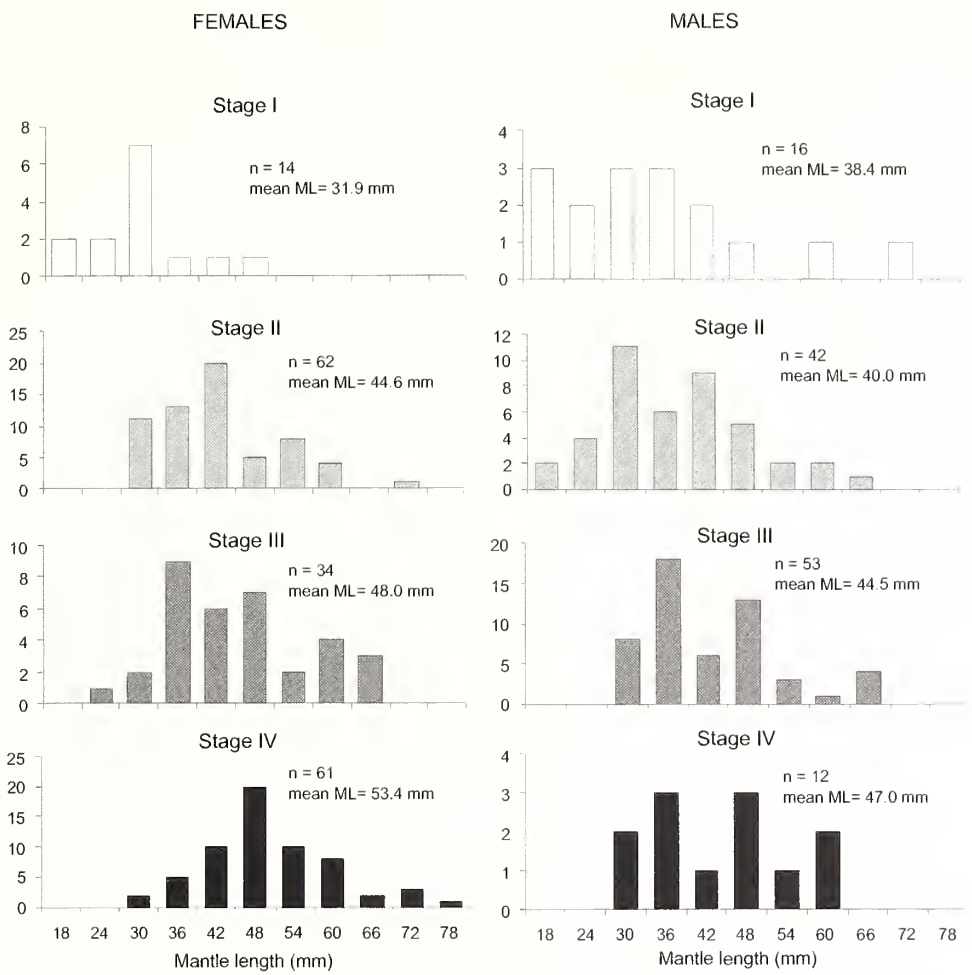

Figure 1. Frequency of mantle length (ML) classes in each maturity stage of females and males of *Octopus tehuelchus* in southern Brazil.

Table 5. Variation in the number and maximum diameter (MDO) of intraovaric oocytes in females of *Octopus tehuelchus* in different maturation stage (Stages I, II, III and IV) in southern Brazil.

	Stage I	Stage II	Stage III	Stage IV
Number of females	12	56	22	45
Mean female ML (± SD) (mm)	32.8 ± 7.4	43.9 ± 9.5	46.6 ± 9.1	48.5 ± 8.4
Range oocytes number	50 to 350	65 to 514	20 to 410	112 to 448
Mean oocytes number (± SD)	139.7 ± 76.6	226.9 ± 108.0	205.1 ± 93.3	267.1 ± 83.5
Range MDO (mm)	0.2 to 3.0	1.0 to 7.4	1.8 to 10.8	1.5 to 13.9
Mean MDO (± SD) (mm)	1.4 ± 0.7	3.1 ± 0.8	5.5 ± 1.8	8.0 ± 2.2

to 62 (21.2 ± 12.3), with maximum length ranging from 1.7 to 57.4 mm (21.2 ± 8.9). Non-significant correlation was found between the number of spermatophores and the ML (r = 0.086) (Figure 5) nor between the length of the spermatophores and the ML (r = 0.03).

Spawning and Hatchlings: All the egg clutches were observed in gastropod shells of *Tonna galea* and *Adelomenon brasiliana*. The number of eggs attached to the shells ranged from 86 to 237 (165.2 ± 60.5; n = 4). The maximum diameter of these eggs ranged from 8.1 to 14.4 mm and their diameter distribution were unimodal.

Recently hatched octopuses (n = 16) resembled small adults, and measured from 5.0 to 6.40 mm ML and from 10.5 to 15.0 mm TL and weighed from 0.07 to 0.12 g (Table 6). During one of the cruises, a spawned female with her eggs stuck to a gastropod shell was placed inside a recipient with sea water and some eggs hatched. Recently hatched octopus did not show any swimming behavior, remaining near the bottom of the recipient.

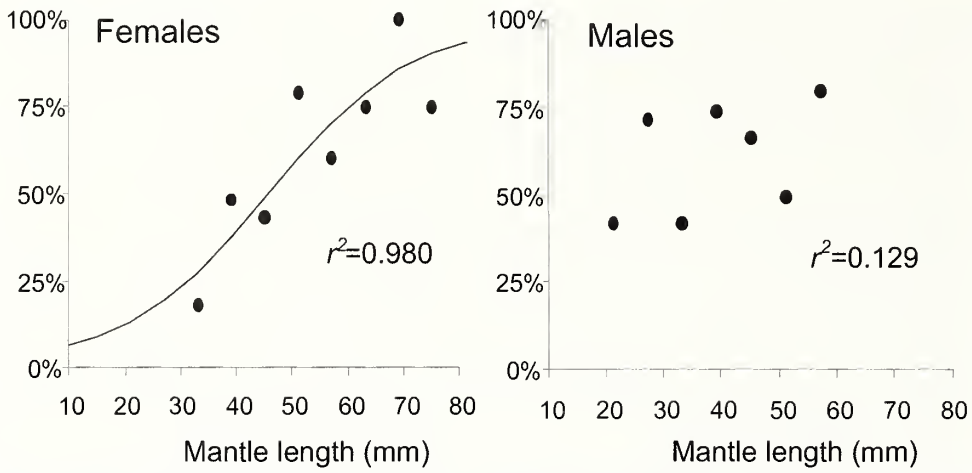

Figure 2. Relative frequency curve of mature individuals by mantle length (ML) classes (mm), of females and males of *Octopus tehuelchus* in southern Brazil adjusted to a logistic model.

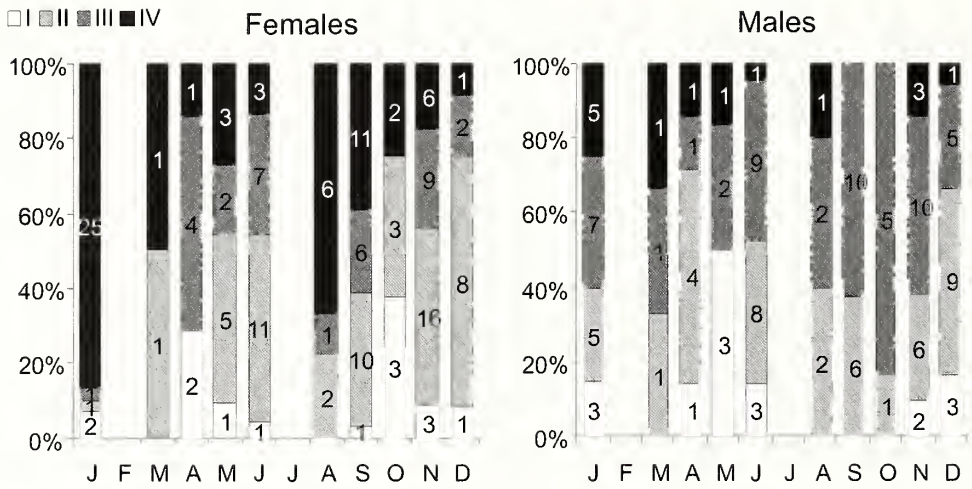

Figure 3. Monthly frequency (%) of the maturity stages of *Octopus tehuelchus* females and males in southern Brazil (values in the bars indicate the number in each stage).

Digestive Gland Index and Reproductive Investment: The digestive gland weight (DGW) of females increased significantly with sexual maturation ($p < 0.05$). The digestive gland index (DGI) was significantly lower in stage I ($p < 0.05$), and remained constant in the others stages (Figure 6). Monthly DGI of females did not follow a seasonal pattern: the lowest values were observed in April and May and the highest ones, in January, March, August, and December (Figure 7).

Digestive gland weight and index of males did not show significant changes along maturation ($p > 0.05$), although small decrease in DGI means along maturation was observed (Figure 6). Seasonally, higher DGI values were observed in spring (Figure 7).

DISCUSSION

Octopus tehuelchus is a small species with large eggs and low fecundity, endemic to the subtropical and temperate waters of the southwestern Atlantic continental shelf (Haimovici and Perez, 1991; Ré, 1998). This study shows that its reproductive biology can adapt to both environments, with seasonal spawning in temperate waters and year round spawning in subtropical environments. Temperature, light intensity and daily photoperiod can influence growth and reproduction in cephalopods (Mangold, 1987). However, these factors may influence particular species or populations in different ways (Boyle and Rodhouse, 2005). Temperature an photoperiod differ between northern Patagonia (40° to 42° S), where daylight ranges from 9 to 15 h and air temperatures along the San Antonio Bay coast range between 6° C and 24° C (Iribarne, 1991) and southern Brazil (32° S), where daylight ranges from 10 to 14 h (Bakun and Parrish, 1990) and bottom temperatures on the continental shelf range between 12° C and 24° C (Haimovici et al., 1996). Although not discriminating the effects of each factor, Iribarne (1991) observed that high intensity of light

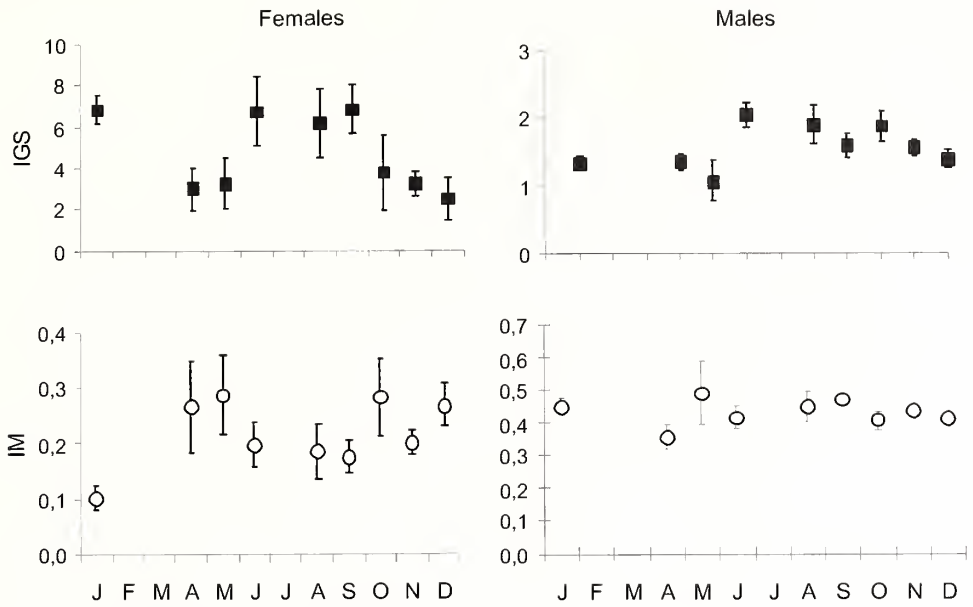

Figure 4. Monthly trends of mean (±SE) values of the gonadosomatic index (GSI) and the maturity index (MI) of *Octopus tehuelchus* females and males in southern Brazil.

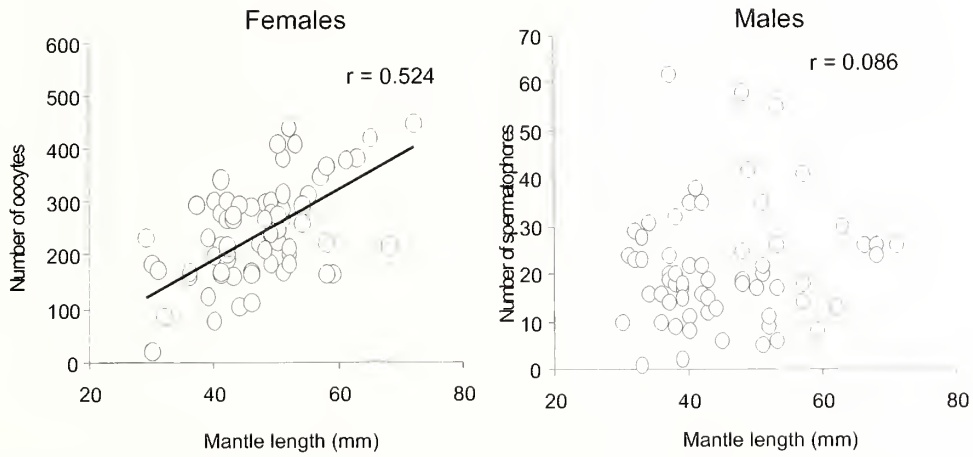

Figure 5. Relationship between mantle length (ML) and potential fecundity (number of developing oocytes and spermatophores) of mature females and males of *Octopus tehuelchus* in southern Brazil.

Table 6. Variation in the number and maximum diameter of eggs (MDE) and in the mantle length (ML), total length (TL) and total body weight (BW) of hatchling on four egg clutches of *Octopus tehuelchus* in southern Brazil compared to northern Patagonia. (Iribarne, 1991; Ré, 1998).

	Southern Brazil	Northern Patagonia
Maximum of eggs per clutch	237	227
Mean egg clutch fecundity (± SD)	165.15 ± 60.84	No data
Range MDE (mm)	8.13 to 14.44	9.0 to 12.0
Mean MDE (± SD) (mm)	10.33 ± 1.09	9.87 ± 0.61
Measured hatchling	16	280
Mean hatchling ML (± SD) (mm)	5.77 ± 0.46	6.64 ± 0.38
Mean hatchling TL (± SD) (mm)	12.06 ± 1.06	14.23 ± 0.83
Mean hatchling BW (± SD) (mg)	0.095 ± 0.014	0.139 ± 0.019

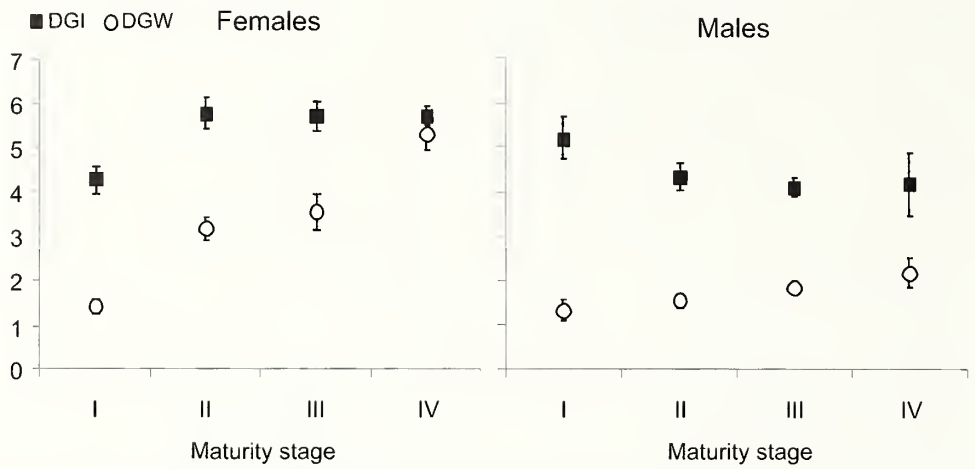

Figure 6. Mean (±SE) of digestive gland weight (DGW) and digestive gland index (DGI) in each maturity stages of *Octopus tehuelchus* females and males in southern Brazil.

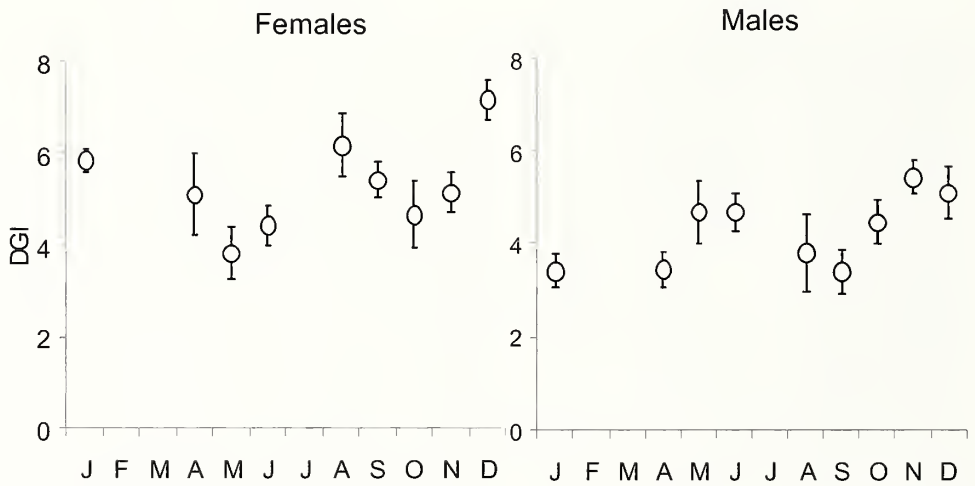

Figure 7. Monthly trends of mean (±SE) values of the digestive gland index (DGI) of *Octopus tehuelchus* females and males in southern Brazil.

and temperature were assoeiated to the intensification of growth and sexual maturation of *Octopus tehuelchus* in northern Patagonia, where sexual maturation oeeurs between December and May and spawning oeeurs from June to November (Pujals, 1982; Ré 1989). More recently, Storero et al. (2010) observed two distinet sub-annual cohorts in the mantle length distributions within San Antonio Bay, suggesting that *O. tehuelchus* can have a more extended spawning season even in the higher latitudes of its distribution. In eontrast, in southern Brazil, mature males and females were observed year-round and egg broods were sampled both in cold and warm months.

Octopus tehuelchus uses a wide variety of bottoms types to deposit eggs. On the rocky bottoms of San Matias Gulf (41° to 42° S), the eggs are attached directly to the substrata (Ré, 1998). On the sandy bottoms of the San Antonio Bay (40°40′ S), the eggs are attached to shelters, mainly bivalve shells of *Ostrea puelchana, Ammiantis purpurata, Mytilus edulis platensis, Chlamys tehuelchus,* and *Pitar rostratus* or gastropod shells of *Buccinanops gradatum, Odontocymbiola subnodosa,* and *Zidona dufresnei* (Iribarne, 1990). Although most of these mollusks also oeeur in southern Brazil (Rios, 2009), egg laying of *Octopus tehuelchus* in this region was found only inside shells of large sized gastropods *Tonna galea* and *Adelomenon brasiliana.* Iribarne (1990) notes that the abundanee of small shells in San Antonio Bay eould favor the seleetion of smaller oetopuses. However, the availability of larger shells in southern Brazil does not seem to have favored larger individuals in this region.

In southern Brazil, a wide range of sizes of developing intraovarie ooeytes and of egg sizes in the egg elutehes (Figure 8) were observed. In northern Patagonia, some females also showed ooeytes at different stages of development (Pujals, 1982). These wide ranges in oocytes size may deerease eompetition among siblings. However, there are differenees in the evolution of the

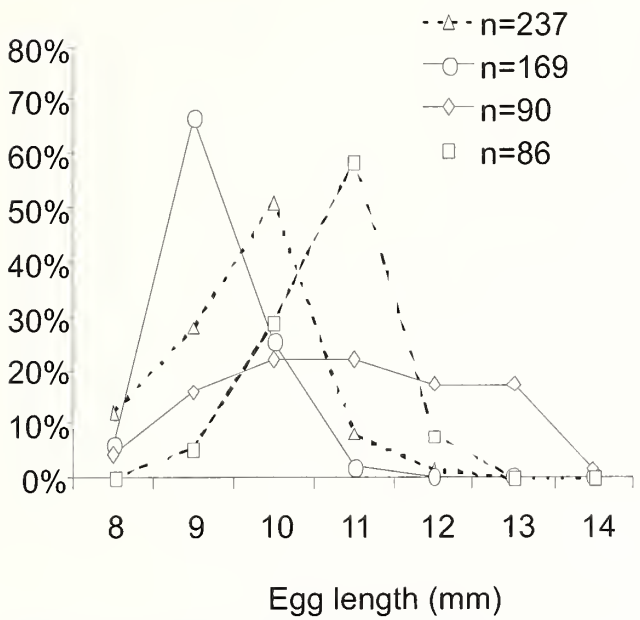

Figure 8. Frequency of spawning eggs size in four egg clutches of *Octopus tehuelchus* in southern Brazil.

DGI between regions, that suggest that the individual spawning period may be longer in southern Brazil: in northern Patagonia, the DGI decreases along sexual maturation and can be associated to intense reserve mobilization along a short spawning season (Pujals, 1982; Iribarne, 1991); in southern Brazil, the DGI remains high along maturation, suggesting accumulation of reserves for a longer period of spawning and parental care of the eggs. However, it is not consensual that the digestive gland has an important role in energy storage in cephalopods, as many authors also consider the reserves in the muscle and gonads (Moltchaniwskyj and Semmens, 2000; Rosa et al., 2004; Semmens et al., 2004).

In males, the DGI decreases in both regions, characterizing a larger mobilization of energy reserves for the reproduction and anticipation of sexual maturation rather than growth (Iribarne, 1991). Moreover, males mature at smaller sizes than females in both areas (Ré, 1989). In the San Matias Gulf, females mature up to three months after males. After copulation, the sperm is stored in the oviducal glands of females (Ré, 1998).

The lack of seasonality in the spawning in southern Brazil may be associated to year-round availability of food for hatchlings. Productivity on the inner shelf of southern Brazil is relatively high (Ciotti et al., 1995), mostly as a consequence of the nutrient-rich runoff from the La Plata River and Patos Lagoon (Piola et al., 2005). In this region, other neritic cephalopods such as *Doryteuthis(Loligo) sanpaulensis* spawn year-round (Andriguetto and Haimovici, 1991; Haimovici, 1998a) and many bony fishes are multiple spawners (Haimovici, 1998b). In the Patagonian gulfs, productivity is dependent on tidal fronts and shows a strong seasonal variation, where higher productivity rates are concentrated in spring and summer (Acha et al., 2004). In temperate environments, such as the northern Patagonian gulfs, seasonality in productivity limits food availability and consequent survival and growth for young octopus in the cold season more difficult. Furthermore, according to Klaich et al. (2006), food intake, growth, and food conversion of *O. tehuelchus* in experimental conditions were lower at 10°C when compared to 15°C.

Based on our data, we have concluded that *O. tehuelchus* has the potential for year round spawning, but ecological constrains such as temperature, which influences metabolism, and photoperiod, which influences productivity, enables the species to express this potential only in the lowest latitudes of its distribution range.

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Two new species of Admetinae (Gastropoda: Cancellariidae) from the northeastern Pacific Ocean

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ABSTRACT

Two new species of the cancellariid subfamily Admetinae are described from bathyal depths of the northeastern Pacific Ocean. *Admete verenae* is presently known only from the hydrothermal vents of the Juan de Fuca Ridge, at depths of 2192 to 2415 m. It differs from other *Admete* in having a large shell with a high spire, strong spiral sculpture, and anteriorly tapering aperture with a deflected siphonal canal and a distinctive siphonal fasciole. Egg capsules, each containing 5–8 embryos, are broadly oval, V-shaped in end view, and raised on a short, broad stalk. *Neadmete ahoi*, from off northern California and Washington State at depths of 276 to 732 m, may be recognized by its distinctive tabulate spire profile and broad, strongly channeled sutural ramp, as well by its anteriorly tapered aperture.

Additional keywords: Mollusca, Neogastropoda, *Admete*, *Neadmete*, Bathyal, hydrothermal vents, egg capsules

INTRODUCTION

The Cancellariidae are a large and diverse family of neogastropods characterized by a highly specialized anterior alimentary system adapted for suctorial feeding. The majority of species are tropical or temperate, but members of the subfamily Admetinae inhabit soft sediments at subtidal to hadal depths in polar regions and intervening deeper waters. Some southern hemisphere admetines share a distinctive radular morphology (Oliver, 1982). Other austral species as well as all boreal Admetinae studied to date lack a radula, but retain a distinctive jaw with its distal portion joined ventrally to form a tube (Harasewych and Petit, 1986). Admetines are neither common nor diverse in the North Atlantic (Bouchet and Warén, 1985:257; Høisæter, 2011), but are more widespread and represented by greater numbers of named species and genera in the fauna of the northern Pacific Ocean (Abbott, 1974; Higo et al., 1999; Kantor and Sysoev, 2005).

Over the past several years, we have received samples of two distinctive species of Admetinae. One was collected during a series of research cruises to the hydrothermal vents along the Juan de Fuca Ridge off British Columbia, and provided by Dr. Verena Tunnicliffe of the University of Victoria, Canada. The other was obtained from commercial fishing vessels working off the coast of Washington State, USA, by Mr. Jon Aho. These two new species are described herein. Abbreviations: CMN: Canadian Museum of Nature, Ottawa; USNM: National Museum of Natural History, Smithsonian Institution, Washington, DC.

SYSTEMATICS

Family Cancellariidae Forbes and Hanley, 1851
Subfamily Admetinae Troschel, 1865 (as Admetacea)

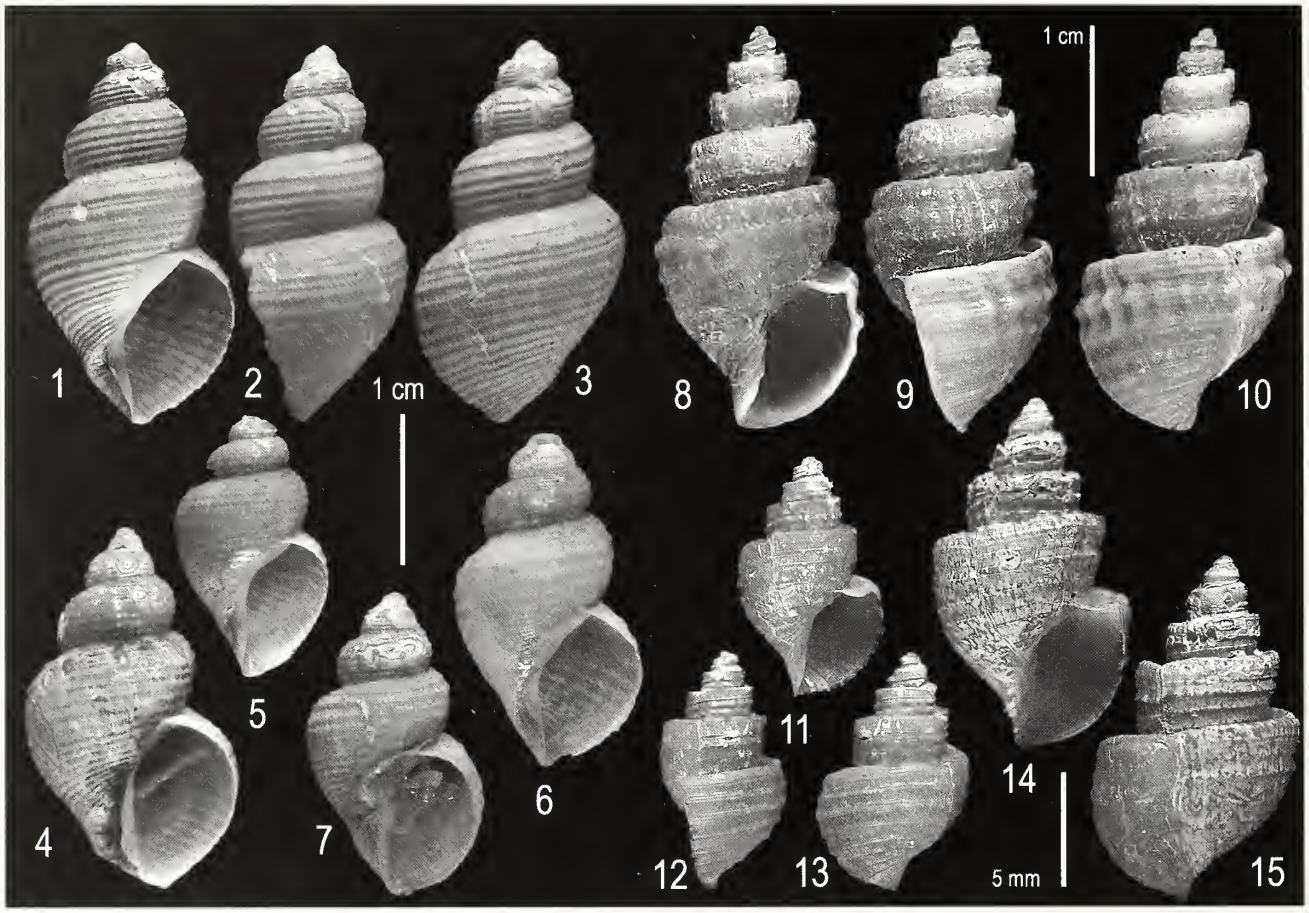
Genus *Admete* Kröyer *in* Möller, 1842

Admete Kröyer *in* Möller, 1842.

Type Species: *Admete crispa* Möller, 1842 (= *Tritonium viridulum* Fabricius, 1780), by monotypy.

Admete verenae new species
(Figures 1–7)

Description: Shell (Figures 1–7) moderately large (to 25.6 mm), thin, with tall, stepped spire (spire angle 44–51°), broadly ovate aperture, and short, tapering siphonal canal. Protoconch unknown, early whorls eroded in all specimens. Teleoconch of 6+ weakly shouldered whorls, becoming more rounded with increasing shell size. Suture minutely impressed. Spiral sculpture of: 2–3 weak cords between suture and shoulder; strong cord along shoulder; 16–18 low, broad, rounded cords between shoulder and siphonal canal; 3–4 finer cords on siphonal canal. Cords slightly broader than intervening spaces, both cords and intervening spaces becoming progressively narrower toward siphonal canal. Five cords between suture and shoulder of penultimate whorl. Axial sculpture of very fine prosocline growth



Figures 1–15. Species of *Admete* and *Neadmete*. **1–7**. *Admete verenae*, new species. **1**, Apertural, **2**, lateral, and **3**, dorsal views of the holotype, USNM 1150387. Apertural views of **4**, paratype 1, **5**, paratype 2, **6**, paratype 3, USNM 1150388, and **7**, paratype 4, USNM 1150389. All from Chowder Hill, HHF, Middle Valley, Juan de Fuca Ridge, 48°27.50′ N, 128°42.50′ W, in 2415 m. Collected by ROV Ropos. **8–15**. *Neadmete ahoi*, new species. **8**, Apertural, **9**, lateral, and **10**, dorsal views of the holotype, USNM 1150394, from off southwestern Washington State, in 457–732 m. **11**, Apertural, **12**, lateral, and **13**, dorsal views of paratype 1, **14**, Apertural and **15**, dorsal views of paratype 2, USNM 1150395, trawled on mud bottom west of Crescent City, California (41°45.91′ N, 124°28.97′ W), in 276 m, R/V Miller Freeman (NOAA), on large dead chunks of the hexactinellid sponge *Aphrocallistes vastus*.

lines. Weak axial ribs produeing tubereles along spiral cord on shoulder (18–20 per whorl) present in uneroded portions of first 3–4 whorls. Aperture broadly ovate, broadest just below shoulder, tapering anteriorly, deflected from coiling axis by 18–22°. Outer lip broadly rounded, weakly corrugated, reflecting spiral sculpture. Parietal region nearly straight to weakly rounded, forming angle of 132–136° with columella at siphonal fascicole. Columella very weakly sigmoidal, nearly straight with 1–2 barely pereeptible eolumellar folds. Inductural area with thin glaze to weak eallus that continues along columella, flaring over pseudoumbilicus before forming weak siphonal fold at juncture with siphonal canal. Siphonal canal short, broad, slightly deflected to the right, forming distinctive siphonal fasciole. Shell color white to cream inside and out. Periostracum thin, lamellose, yellowish to amber in color. Shell strongly eroded, reinforced from within in areas where periostracum worn or absent. Operculum absent.

Anatomy: Anatomieal observations are based on the holotype (♂) and paratype 3 (♀). General anatomieal features as in *Admete viridula* (see Harasewych and Petit, 1986). Preserved animal eomprises 2 ½ to 3 whorls; mantle cavity spans ½ whorl, kidney 1/6 whorl, digestive gland 2 whorls. Foot broad anteriorly, tapering posteriorly, uniformly golden tan in color without discernible eolor pattern. Tentaeles are short, tubular, right longer and narrower than left, eyes absent. Mantle edge is thickened, smooth, siphon short, distinct. Osphradium long, narrow (L/W ~ 6), with 28 leaflets below, 35 leaflets above broad ganglion. Leaflets low, narrow twiee as broad as ganglion above, equal to ganglion below. Ctenidium as wide and about twice as long as osphradium, extending beyond its anterior and posterior margins. Leaflets narrow, deeply pendant. Hypobranehial gland voluminous, as broad as osphradium and ctenidium, thiek, transversely pleated. Pallial gonoduets and reetum run along right side of mantle eavity, partially covered by hypobranchial gland. Kidney only slightly larger than

perieardium. Proboseis short, broad, pleurombolic, with long retractor museles extending to columellar muscle. Bueeal mass small, anterior dorsal surfaee eovered by thin, eutieularized jaw that forms long, thin tube extending toward mouth. Radula absent, paired salivary and aeeessory salivary glands present, very narrow, tubular. Valve of Leiblein at rear of buccal mass. Esophagus extends posteriorly, passing through nerve ring, running posteriorly to join thin, U-shaped stomaeh that lines anterior wall of digestive gland. Intestine rums along right wall of mantle eavity, expanding to form reetum. Penis large, long, broad, thick, with a terminal papilla eminating from an obliquely truncated distal surfaee. Female pallial gonoduct of albumen gland, large eapsule gland, small bursa copulatrix.

Egg Capsules: Several egg capsules, reeently hatehed, were eolleeted at the type locality. Capsules were 5 ¼ mm wide, 4 ½ mm tall, 2 mm wide, oval in profile, V-shaped in end view, and raised above substrate by short (1.5 mm), broad (4 mm), ribbon-like stalk. The long axis of the capsule was tilted with respeet to substrate. The dorsal surfaee (between and just below the free ends of V) has a large, round hatching aperture nearer to the side of capsule tilted toward substrate. Capsules eolleeted at the Grotto Vent site were smaller, but with similar proportions, and contained 5–8 embryos per capsule.

Type Locality: Chowder Hill, Middle Valley, Juan de Fuca Ridge, 48°27.50′ N, 128°42.50′ W, in 2,415 m. Colleeted by ROV ROPOS.

Type Material: Holotype ♂ (length = 25.6 mm), USNM 1150387; paratypes 1–3, USNM 1150388, all from the type loeality (Clam bed seoop 1), collected 22 June 1992, University of Victoria coll. R192-360; paratype 4, USNM 1150389; paratypes 5–6, CMNML 094280, all from the type locality (Clam bed scoop 2), eollected 22 June 1992, University of Victoria coll. R192-361. USNM 1150392, Egg capsules, from the type locality (Clam bed scoop 2), collected 22 June 1992, University of Victoria coll. R192-2230.

Other Material Examined: USNM 1150390, (9 specimens), Finn Vent, Mothra Field, Endeavour Segment, Juan de Fuca Ridge, 47°55.44′ N, 129°06.53′ W, in 2281 m, collected 19 July 1999, University of Victoria eoll. R507-8204; USNM 1150391, (5 speeimens), Grotto Vent (chimney side) Main Field, Endeavour Segment, Juan de Fuea Ridge, 47°57.10′ N, 129°06.00′ W, in 2192 m, collected 16 July 1991, University of Victoria coll. A2409-363; USNM 1150393, egg eapsules, Grotto Vent (ehimney side) Main Field, Endeavour Segment, Juan dc Fuea Ridge, 47°57.10′ N, 129°06.00′ W, in 2192 m, eolleeted 16 July 1991, University of Victoria coll. A2409-2232, eolleeted by ROV Ropos.

Etymology: This new species honors Dr. Verena Tunnicliffe, of the Sehool of Earth and Ocean Sciences, University of Victoria, for her contributions to the study of the ecology and evolution of the deep sea and hot vent biota.

Comparative Remarks: *Admete verenae* is readily distinguished from its eongeners by its large size, high spire, anteriorly tapering aperture with a short siphonal eanal slightly deflected to the right, and conspieuous siphonal faseiole. *Admete viridula* (Fabricius, 1780) and several nominal species to which it is closely related have axial sculpture on the early whorls that sometimes continues onto the posterior portion of later whorls. *Admete regina* Dall, 1911, (Macginitie, 1959: pl. 5, fig. 1), which may be as large or larger, has a weak siphonal fasciole, but differs in having a much broader, generally heavier shell with a proportionally shorter spire, much weaker and finer spiral sculpture, and a much larger, rounder aperture with a concavely curved columella. *Admete brunni* Knudsen, 1964, from 6660–6770 m in the Kermadee Trench, is similar in size, but has a very thin shell with numerous (~50) very fine and faint spiral threads, a larger, more evenly ovate aperture, and a longer siphonal canal that erosses the coiling axis of the shell and lacks a siphonal fasciole.

The egg eapsules of *Admete verenae* are similar to those of *Admete viridula* (illustrated by Bouehet and Warén, 1985: fig. 687), but differ in being flatter, and elevated on a short, broad stalk, with a hatching aperture that is not medial but displaced laterally. The number of embryos per eapsule (5–8) is comparable to that of other admetine speeies (Pawlik et al., 1988: 52).

Identical egg capsules colleeted by DSV Alvin on the Endeavour Segment of the Juan de Fuca Ridge were deseribed and illustrated by Gustafson, Littlewood and Lutz (1991: 39, figs. 22–25), who attributed them to the genus *Admete*, but noted that no species of *Admete* had been eollected from the Juan de Fuca Ridge. These capsules, which contained 1–6 large larvae that complete development within the egg capsule, can now be attributed to *Admete verenae*, suggesting that this species has a paucispiral protoconch.

Genus ***Neadmete*** **Habe, 1961.**

Type Species: *Neadmete okutanii* Petit, 1974, by I.C.Z.N, 1986.

Neadmete ahoi **new species**
(Figures 8–15)

Description: Shell (Figures 8–15) large for genus (to 26.9 mm), moderately thick, with tall, tabulate spire (spire angle 46–58°), sharply angled shoulder, ovate aperture, and short, siphonal eanal. Protoconch unknown, early whorls eroded and pitted in all specimens. Teleoeonch of 6+ strongly shouldered whorls. Suture weakly adpressed and incised. Spiral sculpture: absent in broad channel between suture and shoulder, strong eord at shoulder, 7–8 strong eords between shoulder and siphonal canal, 4–5 weaker cords on siphonal eanal, with 0–3 finer threads between strong cords. Cords

much narrower than intervening spaces, becoming weaker toward siphonal canal. Three cords between suture and shoulder of penultimate whorl. Axial sculpture of fine prosocline growth striae. Axial ribs (18–20 per whorl) appear by whorl 5, extend from shoulder to mid-whorl, forming raised tubercles on intersection with spiral cords. Tubercles appear on shoulder, are strongest on first spiral cord, reduced on second spiral cord, indistinct or absent on other cords. Aperture ovate, tapering anteriorly, deflected from coiling axis by 25–29°. Outer lip slightly prosocline, smooth, with porcellaneous glaze weakly furrowed beneath shoulder and major cords. Parietal region short, weakly rounded, forming angle of 137–141° with columella. Columella nearly straight, axial, with 2 weak oblique columellar folds posteriorly, 2 stronger cords anteriorly, and a pronounced siphonal fold. Siphonal canal short, broad, slightly deflected to the left, crossing the coiling axis of the shell. Shell straw caramel colored externally, with white aperture. Periostracum thin, lamellose, yellowish. Operculum absent.

Anatomy: The anterior portion of a single, partially preserved female specimen, paratype 2 (figs. 14–15), was available for study. General anatomical features were similar to those of *Admete viridula* (see Harasewych and Petit, 1986). Foot broad anteriorly, tapering posteriorly, body color pale, creamy white, tentacles long, tapering, with large, black eyes at their bases. Osphradium, ctenidium large, hypobranchial gland voluminous. Intestine, long, narrow extending beyond anterior edge of capsule gland and small bursa copulatrix. Proboscis short, containing minute buccal mass. Cuticularized jaw covering dorsal and anterior surface of buccal mass formed anteriorly directed tube. Radula absent.

Type Locality: Off southwestern Washington State, USA, in 457–732 m ["250–400 fathoms"].

Type Material: Holotype (length = 26.9 mm), USNM 1150394, from the type locality. Paratypes 1, 2, USNM 1150395, West of Crescent City, California (41°45.912′ N, 124°28.968′ W), trawled, R/V Miller Freeman (NOAA), 276 m, on large dead chunks of the ridged hexactinellid sponge *Aphrocallistes vastus*, on mud bottom, coll. Roger N. Clark, 1 November, 1999.

Etymology: We take pleasure in naming this species for Mr. Jon Aho of Warrenton, Oregon, who generously made the holotype available.

Comparative Remarks: *Neadmete ahoi* differs from all known species of *Neadmete*, as well as from other admetines, in having a strongly channeled sutural ramp.

Kanakoff and McLean (1966) reviewed the Recent northeastern Pacific species, recognizing *Neadmete modesta* (Carpenter, 1864), *N. circumcinta* (Dall, 1873), and provisionally *N. unalaskaensis* (Dall, 1873) as a possible variant of *N. modesta*, noting that these species were all highly variable in shell proportions, thickness and strength of sculpture. These authors also described *N. sutherlandi*, a Late Pliocene species.

Neadmete ahoi somewhat resembles the holotype of *Neadmete modesta*, but differs in having a strongly tabulate spire profile with a broadly channeled sutural ramp, as well as in having a narrower aperture that tapers anteriorly.

Kanakoff and McLean noted that a characteristic of *Neadmete* is the "continuous spiral sculpture in the columella area, that increases the number of columellar plaits." *Neadmete* species have the two columellar folds and siphonal fold that are typical of cancellariids. In addition, there may be 0–2 thinner, sharper folds posterior to the typical columellar folds that overlay the posteriormost spiral cords of the siphonal canal. These thinner folds are not parallel to the columellar folds or siphonal fold.

Cancellaria turrita Sowerby, 1874, a forgotten taxon that is probably a synonym of *N. unalashkensis*, was described by Sowerby as having a "columella straight with 3 folds." In the next paragraph he continued his description, stating that "the folds on the columella appear to be 6 or 7, through the intersection of the transverse ribs passing into the interior."

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We are grateful to Dr. Verena Tunnicliffe, of the School of Earth and Ocean Sciences, University of Victoria, British Columbia, Canada, for making available the specimens of *Admete verenae*. Appreciation is expressed to William J. Ritter, Astoria, Oregon, USA, for sending us material, and for calling to our attention the existence of *Neadmete ahoi*. We are deeply indebted to Jon Aho and Roger N. Clark for making available the specimens used in this study.

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A new species of *Bathytoma* (Gastropoda: Borsoniidae) from the Philippines

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ABSTRACT

A new species of Borsoniidae, *Bathytoma gordonlarki* new species, is described from the Philippines. Specimens were collected in tangle nets in 300–500 m off Balut Island, which is located on the eastern side of the Celebes Sea. The new species is similar to *B. boholica*, a species collected in the central Philippines. However, *B. gordonlarki* has a broader body and a larger spire angle than *B. boholica*. The discovery of this species is important because it demonstrates that even in areas where the fauna has been studied there remains undiscovered diversity.

Additional keywords: Mollusca, Conoidea, tangle nets, Balut Island

INTRODUCTION

The genus *Bathytoma* sensu lato contains at least 100 valid named species (Tucker, 2004). Two-thirds of these are fossil species with a stratigraphic range from Eocene to the Pleistocene. The other one-third are extant species. Remarkably, about half of the Recent species have been described since 1986, with 14 species new to science introduced between 2004 and 2010. All of these species were described from South African or Indo-Pacific localities.

Bathytoma is an important genus of the Borsoniidae (Tucker and Tenorio, 2009). These mollusks have some of the largest shells among the turrids (sensu lato) and commonly reach 50 mm in shell length. Puillandre et al. (2010) described eleven new species of *Bathytoma* from the western Pacific. They suggested that the large number of previously unrecognized species was due to sympatric and fine-scale allopatric speciation. *Bathytoma* may prove to be a source of unrecognized biodiversity in the deep waters of the Indo-Pacific region. Herein, we describe another new species of *Bathytoma* from the Philippines. The shell morphology of the new species is unique and easily distinguishes it from morphologically similar congeners.

MATERIALS AND METHODS

Specimens of the new species were acquired from local fishermen. These were collected using tangle nets in water depth ranging from 300 to 500 m. They had already been cleaned and were empty shells when received. Measurements made for each specimen included the shell length, shell width, and spire length using methods adapted from Röckel et al. (1995). The spire angle was measured from photographic enlargements.

We also examined three specimens of *Bathytoma boholica* also collected off Balut Island in deep water (Santa Barbara Museum of Natural History, SBMNH 424101–424103). Spire angles were measured from images of the holotype of *B. boholica* (Zoologische Staatssammlung München, ZSM 1877), of the holotype of *B. badifasciata* (Muséum national d'Histoire naturelle, MNHN IM2007718120), which was collected in 473-505 m, from the Solomon Islands, 9°44′ S, 160°49′ E, and of the holotype of *B. consors* (MNHN IM200718116), which was collected in 520–581 m, from the Solomon Islands, 10°25′ S, 161°20′ E.

SYSTEMATICS

Superfamily Conoidea Fleming, 1822

Family Borsoniidae Bellardi, 1875

Genus ***Bathytoma* Harris and Burrows, 1891**

Nomen novum pro Dolichotoma Bellardi, 1875, *non* Hope, 1839

Type Species: *Murex cataphractus* Brocchi, 1814, by monotypy (of *Dolichotoma*).

***Bathytoma gordonlarki* new species**
(Figures 1–5)

Diagnosis: Species of *Bathytoma* with small or obsolete peripheral gemmules, with broad ovate swollen teleoconch whorls, and spire angle of more than 55 degrees.

Figures 1–11. *Bathytoma* species. **1–5.** *Bathytoma gordonlarki* new species. **1–2, 4.** Holotype, MSI, shell length = 55.9 mm. **1.** Ventral view. **2.** Lateral view showing sinus. **4.** Spire and protoconch. Scale bar = 1 mm. **3.** Paratype, SBMNH 424100, shell length = 51.4 mm. **5.** Paratype SBMNH 424100, ventral view showing columellar plait, shell length = 58.5 mm. **6–9.** *Bathytoma boholica* Parth, 1994. **6.** Holotype, ZSM 1877, shell length = 62.5 mm. **7–9.** SBMNH 424102, shell length = 52.2 mm. **7.** Ventral view. **8.** Lateral view showing the sinus. **9.** Spire and protoconch, scale bar = 1 mm. **10.** *Bathytoma badifasciata* Puillandre et al., 2010, holotype, MNHN IM200718120, shell length = 61.0 mm. 11. *Bathytoma consors* Puillandre et al., 2010, holotype, MNHN IM200718116, shell length = 45.9 mm.

Description: Shell length 43.8–58.2 mm, shell width 21.3–26.2 mm. Shell shape sub-biconic with rounded swollen body whorl (Figure 1). Spire about 27% of shell length. Protoconch diameter 1.2 mm in diameter, of about 2 whorls (Figure 4), smooth, white. Teleoconch of 8.5 (holotype) to 9.75 (largest paratype) whorls. Suture narrowly channeled. Subsutural ramp complex, consisting of an anterior rounded, almost swollen area, mostly covered by a brown band. Posterior half of subsutural ramp set at steep angle and flat, white. This combination produces a subsutural ramp concave in profile (Figures 1, 3). Spiral sculpture of 11–13 spiral cords minutely to distinctly pustulose. Pustules formed at junction of spiral cords and elevated arcuate axial lines that cross whorl top. About six spiral cords present on posterior half of subsutural ramp and about five on anterior convex portion of subsutural ramp. Spiral cords continue onto body whorl where they become less pronounced and somewhat smoother. Peripheral gemmules are absent but there is a narrow row of closely set arcuate folds at junction of the spire and body whorl (Figure 2). Anal sinus deep, U-shaped, set on anterior half of subsutural ramp (Figure 2). Fine growth lines trace former position of anal sinus and continue onto body whorl. Color light- to dark-brown on spire and shoulder. Anterior shell third may also have brown color (Figure 2). This color pattern may be slightly to almost totally absent (Figures 3, 5) or may consist of a distinct brown band (Figure 2). Interior of aperture white. Columellar plait distinct. Plait narrow, oblique to coiling axis, well-developed, about 1.3 mm tall (Figure 5).

Type Material: Holotype (55.9 mm length × 25.2 mm width) deposited at the Philippine Biodiversity Resource Center, Marine Science Institute (MSI), University of the Philippines. Two paratypes deposited at the Santa Barbara Museum of Natural History (SBMNH 424100). Three paratypes are respectively deposited at the Museum of Comparative Zoology, Cambridge (MCZH 372642), Academy of Natural Sciences, Philadelphia (ANSP 425053), and Muséum national d'Histoire naturelle, Paris (MNHN 23281). All type material collected by fishermen using tangle nets.

Type Locality: Off Balut Island, Celebes Sea, Philippines, 5°24′ N, 125°23′ E, 300–500 m depth.

Distribution: The new species is known from Balut Island on the eastern side of the Celebes Sea south of Mindanao, then north to Bohol Island in the central Philippines (Parth, 1994).

Etymology: We honor Gordon Lark on the occasion of his 80th birthday. He was the founding chairman of the Department of Biology, University of Utah. The second author (BMO) is deeply indebted to him for his guidance and friendship over the years.

Remarks: *Bathytoma gordonlarki* new species is similar in coloration to *B. boholica* Parth, 1994 (Figures 6–8) from the Philippines, *B. badifasciata* Puillandre et al., 2010 (Figure 10) and *B. consors* Puillandre et al., 2010 (Figure 11), both from the Solomon Islands. All these species have brown bands developed to one extent or another. The new species, *B. gordonlarki* differs from those three species and all other *Bathytoma* species in shell and spire shape. The body whorl of *B. gordonlarki* is convex with rounded sides, with swollen aspect (Figure 1). All the other species of *Bathytoma* are more slender. Moreover, the spire angle of *B. gordonlarki* is much greater than in the other three similarly colored species. The spire angle of the type series of *B. gordonlarki* averaged almost 57°. It averaged 39° for three specimens of *B. boholica*, 44° for the holotype of *B. badifaciata* (Figure 10) and 46° for the holotype of *B. consors* (Figure 11).

Parth (1994: fig. 2, left) included a specimen of *B. gordonlarki* as a paratype of *B. boholica*. This specimen was collected from Panglao, Bohol Island, with the holotype and other paratypes of *B. boholica*. We were not able to examine the specimen but the illustration is certainly of a typical specimen of *B. gordonlarki*. Parth's holotype (Figure 6) is identical to what we identify as *B. boholica* (Figures 7–9). Sysoev and Bouchet (2001: fig. 96) and Sysoev (2008: pl. 661, fig. 7) also misidentified specimens of *B. gordonlarki* as *B. boholica*. Puillandre et al. (2010: fig. 1.11) illustrated the same specimen that Sysoev and Bouchet did and identified it as *B. boholica*. Confusion with *B. boholica* may be the reason why this large and apparently common species has remained undescribed.

DISCUSSION

Despite describing 11 new species of *Bathytoma* from the Indo-Pacific, Puillandre et al. (2010) considered that the actual species diversity of the genus was still underestimated in the western Pacific. Our contribution adds yet another species to this group. Considering that most of the species of *Bathytoma* have non-plaktotrophic development, which constrains the ranges of individual species (Puillandre et al., 2010), it is likely that continued collecting in other regions of the Philippines and western Pacific will reveal other new species recognizable by conchological and molecular methods.

It is noteworthy that both *B. boholica* and *B. gordonlarki* are sympatric at Balut and Bohol Islands in the Philippines. In contrast, of the 14 species-group taxa found by Puillandre et al. (2010), 11 were mutually allopatric. Like the other species pairs reported by Puillandre et al. (2010), the *boholica-gordonlarki* species pair could also suggest possible sympatric speciation in these deep-water conoideans. However, bathymetric allopatry cannot be eliminated here, as depth estimates from fishermen are often inaccurate.

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A new species of *Eccliseogyra* (Gastropoda: Nystiellidae) from southeastern Brazil

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ABSTRACT

A new species of *Eccliseogyra* from Brazil is described and compared to its most similar congeners: *E. exquisita* Bouchet and Warén, 1986, *E. folini* (Dautzenberg and de Boury, 1897), and *E. pyrrhias* (Watson, 1886).

Additional keywords: Mollusca, wentletrap, southwestern Atlantic, bathyal

INTRODUCTION

The genus *Eccliseogyra* has traditionally been placed in the family Epitoniidae. Clench and Turner (1952: 336–337) proposed the taxon Nystiellinae as a subfamily of Epitoniidae for epitoniid-like species with axially ribbed nuclear whorls that also show an abrupt change in sculpture with first protoconch whorl and "very different" radulae. Nutzel (1998: 89–92) considered the differences strong enough to raise the taxon to family status. Although some of the differences between the two families listed by Clench and Turner and Nutzel are not as clear-cut as they stated (Bouchet and Warén, 1986: 471, 481), I tentatively follow Nutzel's allocation.

The genus *Eccliseogyra* is composed of deep-water species, usually with minute shells. Size and habitat make the acquisition of specimens difficult, and species are rare in collections. The genus is represented in the western Atlantic by four species: *E. formosissima* (Jeffreys, 1884), *E. nitida* (Verrill and Smith, 1885), *E. performosa* (de Boury, 1917), and *E. pyrhias* (Watson, 1886). Other species have been described from the eastern Atlantic (Bouchet and Warén, 1986). However, as was the case with *Eccliseogyra formosissima*, which was discovered off the coast of Louisiana in the Gulf of Mexico (García, 2003), there is a strong possibility that other eastern Atlantic species of *Eccliseogyra* will be found in the western Atlantic.

The *Eccliseogyra* species described herein was collected off the southeastern coast of Brazil in May, 1987, during cruise MD55 of the R/V Marion-Dufresne, operated by Terres Australes et Antarctiques Françaises. It was a joint project of Muséum National d'Histoire Naturelle, in Paris (MNHN; chief scientist Alain Guille) and Universidade Santa Ursula, in Rio de Janeiro (USU; chief scientist Janete M. Ramos). Malacologists on board were Philippe Bouchet, José H. Leal, and Bernard Métivier. The cruise generated many new discoveries of deep-sea biota, including crustaceans (e.g. Manning et al. 1989; Watling and Gerken, 1999), mollusks (e.g. Leal and Bouchet, 1989; Houart 1991; Verhecken 1991; Absalao and Pimenta 2003), and echinoderms (e.g. Albuquerque et al., 2001).

The new *Eccliseogyra* species is most similar to three Atlantic Ocean congeners; *E. exquisita* Bouchet and Warén, 1986 and *E. folini* (Dautzenberg and de Boury, 1897), recorded from the eastern Atlantic, and *E. pyrrhias* (Watson, 1886), from the western Atlantic.

The material representing the new species is deposited at the Muséum National d'Histoire Naturelle, Paris (MNHN), and Museu de Zoologia da Universidade de São Paulo (MZSP). Another abbreviation used in the text is: dd = empty shells.

SYSTEMATICS

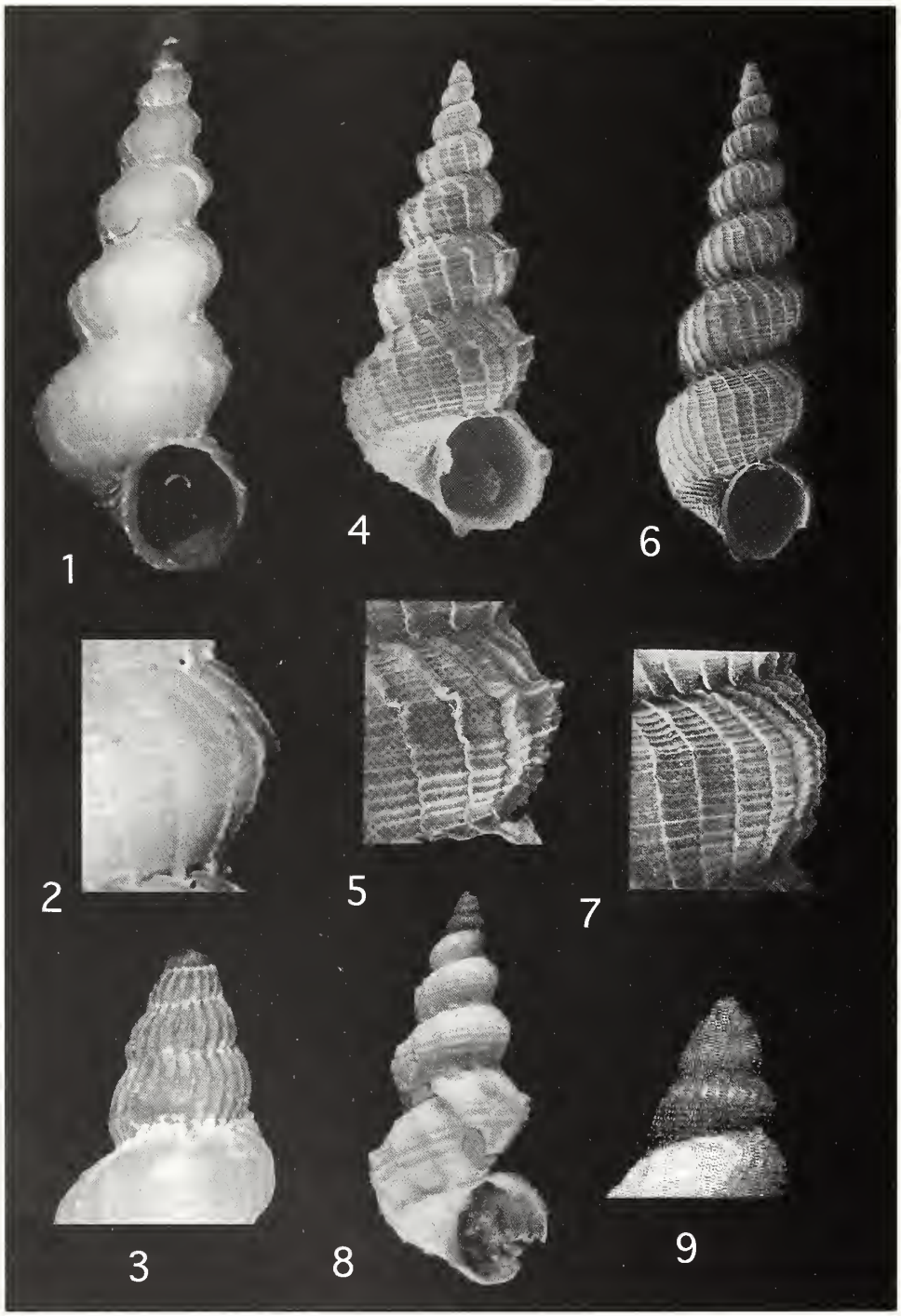
Family Nystiellidae Clench and Turner, 1952

Genus ***Eccliseogyra* Dall, 1892**

Type Species: *Delphinula nitida* Verrill and Smith, 1885 by original designation.

***Eccliseogyra brasiliensis* new species**
(Figures 1–3)

Description: Holotype (Figures 1–3) 8.7 mm in length, thin, rather widely turriculate (width/ length ratio 0.40). Protoconch conical, dark amber in coloration, with nucleus damaged; remaining 3.5 whorls axially ribbed (Figure 4); ribs sigmoid, as wide as interspaces; interspaces spirally striated. Teleoconch of 6 whorls; early whorls strongly convex; subsequent whorls shouldered, roundly angular at periphery. Suture incise. Axial sculpture of widely spaced, low, thin, frilled lamellae; lamellae crossing over suture, some only slightly



Figures 1–9. *Eccliseogyra* species. **1–4.** *Eccliseogyra brasiliensis* new species, holotype MNHN 24428, southeastern Brazil, 21°35′ S, 40°31′ W, 900 m, MD55, sta. CB98, length 8.7 mm, width 3.5 mm. **5–6.** *Eccliseogyra exquisita* Bouchet and Warén, 1986; holotype, Canary Ids., CANCAP st. 4.063; 28°49′ N, 13°42′ W, 875 m, after Bouchet and Warén, 1986, figs.1147–1148, 6.9 mm. **7–9.** *Eccliseogyra folini* (Dautzenberg and de Boury, 1897), lectotype, Monaco st 703; 39°21′ N, 31°06′ W, 1360 m. After Bouchet and Warén, 1986, figs. 1143–1144, 9.1 mm.

peaked at shoulder on last whorl, 20 on penultimate whorl. Spiral sculpture of low, rounded cords; cords of uneven strength, unevenly spaced, weaker below periphery of whorl, not crossing over axial lamellae, about 8 main cords on penultimate whorl. Basal disk posteriorly delineated by weak ridge, ornamented with continuation of axial lamellae and obsolete spiral cords. Umbilicus deep, very narrow. Aperture holostomatous,

subcircular; lip thin; inner lip slightly expanding over umbilical area. Shell white, somewhat glossy. Operculum pale yellow, translucent.

Type Material: Holotype MNHN 24428, length 8.7 mm, width 3.5 mm, MD55, sta. CB98; Paratypes: Paratype 1, MNHN 24429, 21°36′ S, 39°58′ W, 1199–1295 m, 11.4 mm, MD55, sta. CB99; paratype 2, MNHN 24430, 19°38′ S, 38°43′ W, 960 m, 10.5 mm, MD55, sta. CB95; paratype 3, MNHN 24431, 18°59′ S, 37°48′ W, 1540-1550 m, 3 mm, MD55, sta. DC70; paratype 4, MNHN 24432, 19°36′ S, 38°53′ W, 640 m, 9.6 mm, MD55, sta. CB93; paratype 5, MNHN 24433, 19°41′ S, 37°48′ W, 790–940 m, 11.8 mm, MD55, sta. CB77; paratype 6, MZSP 100523, 21°35′ S, 40°31′ W, 900 m, 10 mm, MD55, sta. CB98.

Type Locality: Southeastern Brazil, 21°35′ S, 40°31′ W, 900 m, MD55, sta. CB98.

Other Material Examined: 19°41′ S, 37°48′ W, 790–940 m, MD55, sta. CB77 (2 dd.); 23°47′ S, 42°10′ W, 610 m, MD55, sta. CB105 (5 dd); 21°35′ S, 40°31′ W, 900 m [MD55, sta. CB98] (10 dd).

Distribution: Southwestern Brazil, from 18°59′S to 21°36′ S and from 37°48′ W to 40°31′ W, in 640 to 1550 m.

Remarks: The angular whorls and narrow umbilicus separate the new species from most Atlantic Ocean species of *Eccliscogyra*. From the eastern Atlantic, only *Eccliseogyra exquisita* Bouchet and Warén, 1986 (Figures 4–5) and *E. folini* (Dautzenberg and de Boury, 1897) (Figures 6–7), share these characters. *Eccliseogyra exquisita* is smaller, growing to only 6.9 mm, has 6 teleoconch whorls, a protoconch of only 2.5 whorls (vs. 3.5+ for *E. brasiliensis*), and more obvious shoulder spines (Figure 8). *Eccliseogyra folini* is proportionately narrower (width/length ratio 0.30), has more axial lamellae, more defined spiral cords that keep their strength below the periphery of the whorls, and a more strongly sculptured basal disk.

The western Atlantic species *Eccliscogyra pyrrhias* (Watson, 1846) (Figures 8–9; also see Bouchet and Warén, 1986, fig. 1149) is the most similar. It differs from *Eccliseogyra brasiliensis* in the following features:

1. It has approximately 8 whorls at 8.3 mm; the holotype of the new species has 6 whorls at 8.7 mm, and the largest specimen of *E. brasiliensis* examined (paratype 5), which measures 11.8 mm, has only 7.5 whorls.
2. Its protoconch has more convex whorls (compare Figures 3 and 9). Besides the figured protoconch of the holotype, paratype 3, which also has an almost intact protoconch, has the same outline; several other specimens with damaged protoconchs lack the distinctive strongly convex outline of the last whorl of the protoconch of *E. pyrrhias*.
3. Although teleoconch whorls of juvenile specimens of *Eccliseogyra pyrrhias* and *E. brasiliensis* are very similar, *E. pyrrhias* lacks the spiral ornamentation posterior to the periphery that is present in the new species, and the adult whorls in the latter species are more angular, with a more defined, more concave basal disk.

Etymology: Named for the country in which it was collected.

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Research Note

Clarification of the authorship and date of publication of three Asian species of Unionidae (Bivalvia)

Recently, Petit and Coan (2008) reviewed the molluscan taxa made available in Griffith and Pidgeon (1833–1834), the English translation of Cuvier's *Le Règne Animal* (1830). They determined that plate 21, containing the figures of *Unio leai* (fig. 1), *Unio douglasiae* (fig. 2), and *Unio grayii* (fig. 3), was dated 1833 and that the three species take their date of publication from this date and not the date of the volume [1834]. Petit and Coan reported the correct authorship of the first two species as being Gray in Griffith and Pidgeon, 1833. Haas (1969) listed *Unio leai* as *Lamprotula leai* (Gray in Griffith, 1834) and used *Unio douglasiae* Griffith and Pidgeon, 1834. Correction of authorship and date of publication for these two species does not have any effect on their synonymies.

Unio grayii was the third species illustrated on plate 21, figure 3. This taxon was listed in the index of the Griffith and Pidgeon volume, attributed to Lea, but no geographic location was given. Given that this taxon was attributed to Lea, Petit and Coan (2008) did not discuss it. However, Lea did not describe a taxon *Unio grayii* but did describe *Unio grayanus* Lea, 1834 (see Scudder, 1885). In discussions with Petit and Coan, they confirmed that the figure caption of plate 21 of Griffith and Pidgeon indicates that *Unio grayii* was in fact described by Gray in Griffith and Pidgeon in 1833, and not by Lea as erroneously listed in the index.

The history of the use of *Unio grayii* is examined. Conrad (1853) erected *Lanceolaria* as a subgenus of *Unio* and used *Unio grayanus* Lea, 1834 as the type species. Simpson (1900, 1914) treated *Lanceolaria* as a section of *Nodularia* Conrad, 1853. He listed *Nodularia* (*Lanceolaria*) *grayana* (Lea, 1834) and included "*Unio grayii* Griffith, Grif. Cuv., 1834" as a junior synonym. Haas (1969) recognized *Unio grayana* Lea, 1834 and placed it in *Lanceolaria* as a genus separated from *Nodularia*, but failed to include any mention of *Unio grayii*. Liu (1979) reported *Lanceolaria grayana* from China and included *Unio grayii* as a junior synonym. Đặng et al. (1980) recognized *Lanceolaria grayi* [sic] (Griffith and Pidgeon, 1834) as a species separated from *Lanceolaria grayana* (Lea, 1834) from north Viet Nam.

The correct authorship and date of publication for *Unio grayii* is Gray in Griffith and Pidgeon, 1833. The *Unio grayii* figure is based on a specimen supplied by Gray. A preliminary search by Jonathan Ablett, Mollusk Collections, The Natural History Museum, London, did not produce the type specimen of *Unio grayii*. Đặng (1980) commented that Moskvicheva (1973) separated *L. grayii* with zigzag tubercles and ridges along the dorsal-slope from *L. grayana* with only tubercles and no dorsal ridges.

If these taxa are treated as separate species there is no difficulty. However, if *Unio grayii* is assumed to be synonymous with *Unio grayanus* as used by Simpson (1900, 1914) and Liu (1979), then with the revised date of publication for *Unio grayii*, *Lanceolaria grayii* (Gray in Griffith and Pidgeon, 1833) becomes the senior synonym of *Lanceolaria grayana* (Lea, 1834) based on date priority. This case does not meet both conditions of Article 23.9.1 of the Code of Zoological Nomenclature (International Commission on Zoological Nomenclature, 1999) to preserve prevailing usage of *Unio grayanus* Lea, 1834 as the accepted name because *Unio grayii* has been used in the years after 1899 (see Đặng et al., 1980).

Richard Petit and Eugene Coan are thanked for their time and efforts to help clarify the author and date for *Unio grayii*. Jeffrey T. Garner and Robert Butler are thanked for their clear and careful reviews.

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The Delray Beach, Florida, colony of *Cerion (Paracerion) tridentatum costellata* Pilsbry, 1946 (Gastropoda: Pulmonata: Cerionidae): Evidence for indirect Cuban origins

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ABSTRACT

A large colony of *Cerion* has recently been reported from Delray Beach, Florida, far north from the ranges of both native and introduced species of *Cerion*. Specimens correspond morphologically to the type series of *Cerion (Paracerion) tridentatum costellata* Pilsbry, 1946, which no longer survives at its type locality (Fort Jefferson, Garden Key, Dry Tortugas, Florida.) Historical data indicate that this taxon is a hybrid of two or more of the five Cuban species of *Cerion* introduced to Fort Jefferson by Bartsch in June, 1924. Museum records document that a propagule of this hybrid taxon was transplanted to Boynton Beach in the late 1940s and proliferated to give rise to the Delray Beach colony. Partial cytochrome c oxidase I sequences reveal the Delray colony to be monophyletic, and of exclusively Cuban ancestry. Limited sampling confirms the presence of mitochondrial genes from two (*C. tridentatum* and *C. sculptum marielinum*) of the five Cerion taxa introduced to Fort Jefferson in 1924. A larger sample size, together with data from nuclear genes, will be needed to rule out the presence of rare alleles from other taxa. Transplantation of this newly formed hybrid propagule to an area distant from either parent population has allowed it to evolve in isolation and provides a unique opportunity to study the origins and persistence of genetic diversity within the genus *Cerion*.

Additional keywords: Native species, introduced species, cytochrome c oxidase I

INTRODUCTION

The fossil history of the Genus *Cerion* in Florida dates from the Oligocene/early Miocene (Petuch, 2004: 73), yet the Recent fauna is limited to a single native species with four subspecies or varieties, and to survivors of a series of experimental introductions during the early 20th Century. These introductions and the fates of the resulting colonies were documented in detail by Bartsch (1913–1931), summarized by Pilsbry (1946: 165–169), and reviewed by Harasewych and Strauss (2006: table 1.C., fig. 1).

Harasewych and Strauss (2006) also detailed the occurrence of a well-established yet previously unreported colony of *Cerion* in Delray Beach, Florida, far north from the ranges of either the native or any of the introduced species. These authors conjectured that, "whether transported by a hurricane or intentionally introduced, the most proximal sources for the Delray Beach colony are the *Cerion* faunas of the Little Bahama Bank or of the Bimini Islands." However, comparisons of the shells of both mottled and unpigmented phenotypes from the Delray Beach colony with the primary types of each of the named *Cerion* from the Bimini Islands (5 taxa) and the Little Bahamas Bank (9 taxa) failed to produce a close match, leading Harasewych and Strauss (2006) to speculate that the Delray Beach colony may be a hybrid population descended from two or more propagules introduced some time near the middle of the 20th Century.

In the present study, we investigate more broadly the potential sources of the Delray Beach colony of *Cerion*. Historical records of the various transplantation experiments and relevant museum collections were examined. In addition, partial sequences of the mitochondrial cytochrome c oxidase I gene derived from examples of both white (Figure 1) and mottled (Figure 2) phenotypes were compared against representative *Cerion* taxa spanning the current range of the genus, including the Bimini Islands and Little Bahamas Bank. These molecular data, supplemented by morphological comparisons and archival records, are used to ascertain the identity and sources for this introduced colony.

Figures 1–15. Species of *Cerion* treated in this study. **1–6.** *Cerion* (*Paracerion*) *tridentatum costellata* Pilsbry, 1946. **1.** White and **2.** mottled morphotypes, USNM 1123779. Between highway A1A and the Ocean, at northern limit of public beach, Delray Beach, Florida, Florida (26°28.032' N, 80°3.382' W). On vegetation on seaside sand dunes, within 0.5 m of the ground. M.G. Harasewych coll., July 7, 2008. **3.** Lectotype (here designated), specimen figured in Pilsbry, 1946:fig. 80d. ANSP 179274. **4.** Paralectotype, specimen figured in Pilsbry, 1946: fig. 80c. ANSP 426010. Both from Garden Key, Dry Tortugas, Florida, Bales and McGinty coll., 1941. **5.** White and **6.** mottled morphotypes, ANSP 192703, from the McGinty lawn, Boynton Beach, Florida, Pilsbry coll., April 1954. **7–11.** Taxa introduced to Fort Jefferson, Garden Key, Dry Tortugas, by Paul Bartsch in June, 1924. **7.** *Cerion* (*Paracerion*) *tridentatum* Pilsbry and Vanatta, 1895, USNM 392820, Rincon de Guanaba at Playa, Cuba. Bartsch coll., May 29, 1924. **8.** *Cerion chrysalis* Férrusac, 1832, USNM 361745, Cabañas Fort, Havana Cuba, Bartschcoll., May 27, 1924. **9.** *Cerion sculptum* Poey, 1858, USNM 361763, near Light House, Mariel, Cuba. Bartsch coll., May 29, 1924. **10.** *Cerion mumia* Bruguiere, 1792. USNM 391821, the point at Miramar, Cuba. Bartsch coll., 1924. **11.** *Cerion* "species". USNM 361766, east of the point at Mariel, Cuba, Bartsch coll., 1924. **12–15.** Dried museum specimens of *Cerion* used for DNA extraction. **12–13.** *Cerion* (*Paracerion*) *tridentatum* Pilsbry and Vanatta, 1895, USNM 392820, Rincon de Guanaba at Playa, Cuba. Bartsch coll., May 29, 1924. **14.** *Cerion* (*Paracerion*) *tridentatum costellata* Pilsbry, 1946, USNM 487438a. **15.** *Cerion sculptum* Poey, 1858, USNM 487438b, both from, Garden Key, Dry Tortugas, Florida. G.R. Bales coll., May 3, 1947. Abbreviations: **e,** epiphragm, **t,** dried tissue used for DNA extraction.

MATERIALS AND METHODS

With the exception of the *Cerion* samples from Cuba and Fort Jefferson in the Dry Tortugas, which were available only as dried museum specimens, DNA from each of the taxa listed in Table 1 was extracted from a portion of the digestive gland and gonad dissected from living specimens using a Qiagen DNeasy extraction kit according to manufacturer's protocol.

In order to obtain DNA from older museum specimens, individuals with intact epiphragms were selected, and the dorsum of the shell removed using a Wizard Model 100 Saw (Diamond Pacific Tool Corp.) with a diamond lapidary blade. This usually revealed second, and occasionally third, epiphragms, as well as desiccated tissues (Figure 15). Small fragments of dried digestive gland and gonad were extracted using the Qiagen DNeasy kit. The initial lysis step was extended to 48 hours at 65°C with continuous agitation, until the tissues completely disintegrated. Subsequent steps were according to manufacturer's protocol.

A portion of the mitochondrial cytochrome oxidase 1 gene was amplified using Sigma Jumpstart Red Taq Ready Mix and Folmer et al. (1994) primers. Resulting PCR products were purified using AMPure magnetic beads (Agencourt, manufacturer's protocol) and sequenced using either ABI 3130xl or Spectrumedix 9600 fluorescent sequencers. Sequences were manually checked and assembled using Sequencher 4.6 (Gene Codes Corp.), and aligned against the cytochrome *c* oxidase 1 gene of *Albinaria caerulea* (Deshayes, 1835) (1529 bp) derived from its complete mitochondrial genome (Hatzoglou et al., 1995; GenBank NC 001761) using ClustalX 2.1 (Larkin et al., 2007). The ends and primers were trimmed, yielding an alignment of 655 bases corresponding to positions 39 to 693 of the COI gene in *Albinaria caerulea*. Aligned sequences were reviewed and translated to 218 amino acid sequences using McClade Version 4.08 (Maddison and Maddison, 1992) and the extended *Drosophila* mtDNA genetic code. Relationships among the taxa based on nucleotide and amino acid sequences were analyzed using PAUP 4.0b10 (Swofford, 2002).

RESULTS

Comparative Morphology and Historical Review: Specimens of the Delray Beach colony of *Cerion* (Figures 1, 2) were compared against samples of each of the native and non-native taxa introduced to Florida (Harasewych and Strauss, 2004: Table 1) as well as with *Cerion tridentatum costellata* Pilsbry, 1946, a form that Pilsbry described from Garden Key (Dry Tortugas). The Delray Beach *Cerion* matched closely the type series *Cerion tridentatum costellata*, which also includes both white (Figure 3) and mottled (Figure 4) phenotypes.

There were no native *Cerion* species in the Dry Tortugas prior to Bartsch's introductions during the first quarter of the twentieth century (Bartsch, 1913–1931). The majority of these transplantation and hybridization experiments were conducted on Loggerhead Key, where the Carnegie Institution of Washington maintained its Marine Biology Laboratory from 1903 until 1939. However, *Cerion* were also introduced onto Garden Key, Man Key, Boy Key, and Bird Key in the Dry Tortugas.

Cerion species were introduced onto Garden Key on two occasions. On June 8, 1912, 138 specimens of a species later to be named *Cerion viaregis* Bartsch, 1920 were planted in the "back of a small unpainted house on the northeast side of the Fort, Garden Key, Tortugas." (Bartsch, 1913: 130). Bartsch visited this planting on May 2, 1913, and found 60 of the *Cerion* still living. He concluded that the site was unsuitable for the colony and transplanted the living specimens to the inside of the fort, near the center (Bartsch, 1914a: 170–171). He revisited this colony on April 27, 1914, and discovered that "the second planting inside the fort had been burned over; 28 dead shells were found, but the rest had disappeared. A visit to the original planting showed 6 living specimens, but no young." On January 16, 1919, "a careful search was made both within and without the fort, but not a trace of *Cerion* was discovered, so it is feared that this colony has disappeared." (Bartsch, 1920a: 19–20)

On June 5–20, 1924, Bartsch (1924b: 187) introduced 2,125 specimens of Cuban *Cerion* onto the west and north side of the parapet at Fort Jefferson on Garden Key. These included: 500 specimens of *Cerion tridentatum* Pilsbry and Vanatta, 1895, from Rincon de Guanabon (Figure 7); 500 specimens of *Cerion chrysalis* Férrusac, 1832, from near Cabanas Fort (Figure 8); 500 specimens of *Cerion sculptum* Poey, 1858, from near the lighthouse at Mariel (Figure 9); 500 specimens of *Cerion mumia* Bruguière, 1792, from the point at Miramar (Figure 10); and 125 young specimens of a species of *Cerion* that Bartsch considered to be undescribed (similar to *C. johnsoni*) from east of the point at Mariel (Figure 11). Upon revisiting these colonies the following year, Bartsch (1925a: 222) reported that "the colonies which we introduced on the top of Fort Jefferson last year also showed considerable mortality, also considerable living specimens." In August 1927, the colonies on the parapet were reported to be "holding their own" (Bartsch, 1927: 216). By August 1931, *Cerion mumia*, *C. chrysalis*, and *C. tridentata* were "thriving", while *C. sculptum*, and *C.* n. sp. "seemed not to have survived" (Bartsch, 1931: 373).

In his treatment of the genus *Cerion*, Pilsbry (1946) discussed Bartsch's transplantation experiments in the Florida Keys. Citing a letter from Bartsch, Pilsbry (1946: 166) reported that specimens of *Cerion striatellum* (Guérin, 1829) from Balena Point, near Guanica Bay, Puerto Rico, were also introduced to the parapet at Fort Jefferson in 1924. This species was not

Table 1. Taxa, locality data, voucher specimen information and GenBank Accession information for the samples used in this study. USNM = National Museum of Natural History, Smithsonian Institution.

TAXON	LOCALITY	Voucher Specimen	GenBank Accession Number [CO 1]
DUTCH WEST INDIES			
Cerion uva arubanum (Baker, 1924)	Baranca Alto, Aruba	USNM 1073039	JN 038138
Cerion uva arubanum (Baker, 1924)	Baranca Alto, Aruba	USNM 1073039	JN 038139
FLORIDA			
Cerion Delray White 1	Delray Beach, FL	USNM 1123779	JN 038140
Cerion Delray White 2	Delray Beach, FL	USNM 1123779	JN 038141
Cerion Delray White 3	Delray Beach, FL	USNM 1123779	JN 038142
Cerion Delray White 4	Delray Beach, FL	USNM 1123779	JN 038143
Cerion Delray Mottled 1	Delray Beach, FL	USNM 1123779	JN 038144
Cerion Delray Mottled 2	Delray Beach, FL	USNM 1123779	JN 038145
Cerion Delray Mottled 3	Delray Beach, FL	USNM 1123779	JN 038146
Cerion Delray Mottled 4	Delray Beach, FL	USNM 1123779	JN 038143
Cerion incanum incanum (Binney, 1851)	Key West, FL	USNM 1116902	JN 038147
Cerion incanum incanum (Binney, 1851)	Key West, FL	USNM 1116902	JN 038148
Cerion casablancae Bartsch, 1920 32	Indian Key, FL (*ex* Andros Bahamas)	USNM 1158942	JN 038149
Cerion casablancae Bartsch, 1920 33	Indian Key, FL (*ex* Andros Bahamas)	USNM 1158942	JN 038150
Cerion tridentatum costellatum Pilsbry and Vanatta, 1895	Garden Key, Dry Tortugas, FL 1947	USNM 487438a	JN 038151
Cerion sculptum (Poey, 1858)	Garden Key, Dry Tortugas, FL 1947	USNM 487438b	JN 038152
CUBA			
Cerion tridentatum Pilsbry and Vanatta, 1895	Rincon de Guanaba at Playa, Cuba, 1924	USNM 392820a	JN 038153
Cerion tridentatum Pilsbry and Vanatta, 1895	(source of Garden Key introduction)	USNM 392820b	JN 038153
PUERTO RICO			
Cerion striatellum (Guerin, 1829) 1	Tamarindo Beach, Puerto Rico	USNM 1158944	JN 038154
Cerion striatellum (Guerin, 1829) 2	Tamarindo Beach, Puerto Rico	USNM 1158944	JN 038154
LITTLE BAHAMA BANK			
Cerion bendalli Pilsbry and Vanatta, 1896	Great Abaco, Bahamas	USNM 1158941	JN 038155
Cerion bendalli Pilsbry and Vanatta, 1896	Great Abaco, Bahamas	USNM 1158941	JN 038156
GREAT BAHAMA BANK			
BIMINI			
Cerion biminiense Henderson and Clapp, 1913	Bimini, Bahamas	USNM 1080860	JN 038157
Cerion biminiense Henderson and Clapp, 1913	Bimini, Bahamas	USNM 1080860	JN 038158
Cerion eximium lerneri Clench, 1956	Bimini, Bahamas	USNM 1080858	JN 038159
Cerion eximium lerneri Clench, 1956	Bimini, Bahamas	USNM 1080858	JN 038160
ANDROS			
Cerion pepperi Bartsch, 1913 192	Somerset Pt., Andros, Bahamas	USNM 1080841	JN 038161
Cerion pepperi Bartsch, 1913 193	Somerset Pt., Andros, Bahamas	USNM 1080841	JN 038162
ELEUTHERA			
Cerion uniformis Maynard, 1913	Eleuthera, Bahamas	USNM 1158933	JN 038163
Cerion uniformis Maynard, 1913	Eleuthera, Bahamas	USNM 1158933	JN 038163
Cerion glans Küster, 1844	Eleuthera, Bahamas	USNM 1158937	JN 038164
Cerion glans Küster, 1844	Eleuthera, Bahamas	USNM 1158937	JN 038164
LONG ISLAND			
Cerion malonei Clench, 1937	Long Island, Bahamas	USNM 1083081	JN 038165
Cerion malonei Clench, 1937	Long Island, Bahamas	USNM 1083081	JN 038166
Cerion fernandina Clench, 1937	Long Island, Bahamas	USNM 1083076	JN 038167
Cerion fernandina Clench, 1937	Long Island, Bahamas	USNM 1083076	JN 038167
Cerion josephinae Clench, 1935	Long Island, Bahamas	USNM 1083062	JN 038168
Cerion josephinae Clench, 1935	Long Island, Bahamas	USNM 1083062	JN 038168

(Continued)

Table 1. (Continued)

TAXON	LOCALITY	Voucher Specimen	GenBank Accession Number [CO I]
SAN SALVADOR			
Cerion watlingense Dall, 1905	San Salvador, Bahamas	USNM 1110080	JN 038169
Cerion watlingense Dall, 1905	San Salvador, Bahamas	USNM 1110080	JN 038170
TURKS AND CAICOS			
Cerion regina Pilsbry and Vanatta, 1895 1	Conch Cay, Middle Caicos Island	USNM 1080843	JN 038171
Cerion regina Pilsbry and Vanatta, 1895 2	Conch Cay, Middle Caicos Island	USNM 1080843	JN 038171
Cerion lewisi Clench, 1961 1	Blue Hill, Providenciales	USNM 1080845	JN 038172
Cerion lewisi Clench, 1961 2	Blue Hill, Providenciales	USNM 1080845	JN 038173

mentioned in Bartsch's (1924b: 187) published account of the introductions, and Pilsbry (1946: 166) noted that *C. striatellum* was not represented in the collections made in the Tortugas in 1941 by Dr. Bales and Mr. McGinty.

Working with the 1941 collections from the Tortugas, Pilsbry (1946: 168) reported that no specimens of *C. viaregis* or *C. mumia* were present, and questioned the identity of the species that Bartsch referred to as *C. mumia*. Pilsbry revised the nomenclature for the surviving taxa introduced to Garden Key to: *C. chrysalis fastigatum* Maynard, 1896 and *C. sculptum marielinum* Pilsbry, 1927, commenting that both were abundant on Garden Key in 1941, as was *Cerion tridentatum*. He also noted that the typical smooth form of *C. tridentatum* was rare on Garden Key, and went on to name the prevalent, ribbed form as *Cerion tridentatum costellata*, illustrating three specimens (Pilsbry, 1946: fig. 80, b, c, d) that included both white and mottled phenotypes. The unpigmented specimen (Figure 3) illustrated in (Pilsbry, 1946: fig. 80, d) is selected here as the lectotype (ANSP 179274). The remaining syntypes (Figure 4) become paralectotypes and have been reeatalogued as ANSP 426010.

Additional specimens of living *Cerion tridentatum costellata* and *C. sculptum marielinum* sampled from Garden Key on May 3, 1947, are represented in the collections of the National Museum of Natural History (USNM 487438). A survey of Garden Key by the senior author in July 2006 revealed numerous dead *Cerion* on the parapets of Fort Jefferson, but no living *Cerion* were found anywhere on Garden Key.

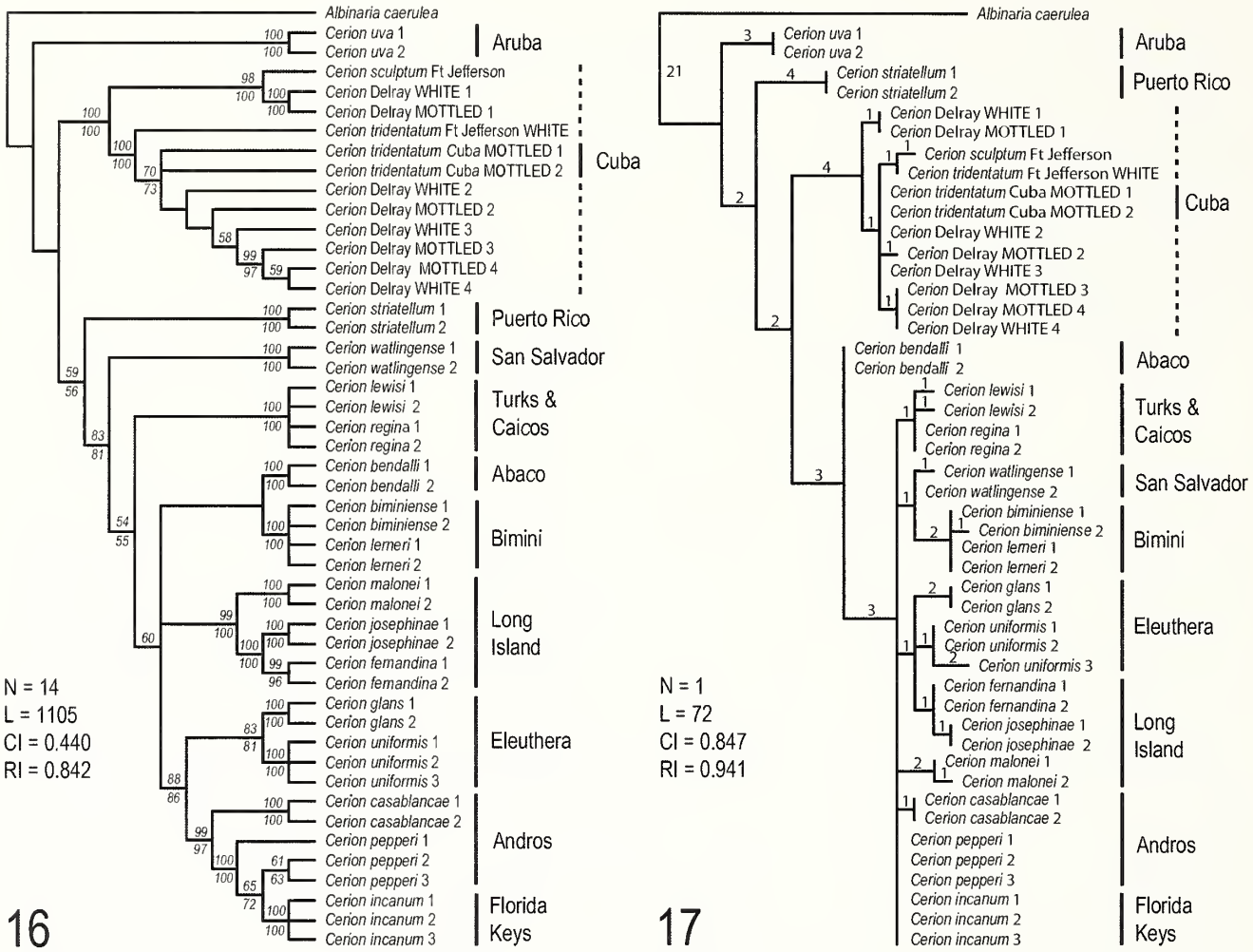
The collections of the Academy of Natural Scienees eontain a lot (ANSP 192703) of several specimens eorresponding to *Cerion tridentatum costellata* colleeted by Pilsbry in 1954. The label, hand written by Pilsbry, identifies the specimens only as *Cerion*, but states that they are from Boynton Beach, Florida, "from the McGinty lawn, April, 1954. Imported from Andros + the Keys 5 or 6 years before." The "McGinty lawn", on Old Ocean Boulevard in Boynton Beaeh, was roughly 3 kilometers north of the Delray Beach population of *Cerion* (Harasewych and Strauss, 2006: 94).

The phenotype *Cerion tridentatum costellata*, which presently inhabits Delray Beaeh, traees its origin to Fort Jefferson, on Garden Key, and may be a hybrid of two or more of five Cuban taxa introduced there by Bartsch in 1924: *Cerion tridentatum*, *Cerion mumia* (identity questioned by Pilsbry), *Cerion chrysalis* (revised by Pilsbry to *C.chrysalis fastigatum*), *Cerion sculptum* (revised by Pilsbry to *C. sculptum marielinum*), and an undescribed taxon of *Cerion* similar to *C. johnsoni*. There are eonflieting reports as to whether the Puerto Rican *Cerion striatellus* was among the species that were introduced to Fort Jefferson, and may have thus eontributed to the genotype.

During the 1940s, propagules of *Cerion* from "the Florida Keys and Andros" Island in the Bahamas were introduced to the McGinty's lawn. While it seems certain that a sample of *Cerion* from Fort Jefferson was among those introduced to Boynton Beach, it is less clear how many, if any, of the four native and 13 introduced species from the Florida Keys (Harasewych and Strauss, 2006: Table 1) or the 26 named species from Andros Island (see Harasewych, 2009) were also introduced to Boynton Beach, and thus may have contributed to subsequent hybridizations.

Evidence From Partial Cytochrome c Oxidase I Sequences: The strict consensus of six most parsimonious trees based on maximum parsimony analyses of a 655 bp segment of the cytochrome c oxidase I gene (Figure 16) groups individuals from the same taxon, as well as taxa inhabiting the same island (e.g., Long Island, Eleuthera) or island group (e.g., Bimini Islands, Turks and Caicos Islands) with a high level of support.

All Delray specimens, both mottled and white, emerged in a single, highly supported clade that also included two Cuban specimens of *Cerion tridentatum* (Figures 12, 13) from the same 1924 sample as the 500 individuals of this species that were introduced to Fort Jefferson, as well as a specimen of *C. tridentatum*



Figures 16–17. Relationships of the Delray Beach population of *Cerion*, based on maximum parsimony analyses of a 665 bp segment of the cytochrome c oxidase I gene (CO I) using representative taxa spanning the geographic range of the genus. **16.** Strict consensus of 6 most parsimonious trees, bootstrap proportions given in % above, and jackknife proportions given in % below nodes supported at levels above 50%. **17.** Single most parsimonious tree based on amino acid sequences translated using the *Drosophila* mtDNA (extended) genetic code.

costellata (Figure 14) and of *Cerion sculptum marielinum* (Figure 15) that were collected on Garden Key in 1947. This clade is comprised of two subclades, each also highly supported. One includes the specimen of *Cerion sculptum marielinum* and two Delray specimens, one white, the other mottled. The other subclade includes the two 1924 specimens of *Cerion tridentatum*, the 1947 specimen of *C. tridentatum costellata*, and the remaining six Delray specimens, three white and three mottled. These data indicate that both *C. tridentatum* and *C. sculptum marielinum* have contributed to the genotype of *C. tridentatum costallata* at Fort Jefferson, and that traces of both parent taxa persist in the mitochondrial genomes of the Delray Beach population in a 3:1 ratio after more than 60 years. As none of the Delray specimens (n = 8) appeared elsewhere in the tree, there is no evidence to indicate that other Floridian or Andros Island taxa have contributed to, or persist in, the genotype of the Delray Beach population. However, a substantially larger sample size, and data from nuclear genes would be needed to rule out the presence of rare alleles from other taxa.

The nucleotide sequences were translated to amino acids, and the maximum parsimony analysis repeated, resulting in a single most parsimonious tree (Figure 17).

Neither individuals of the same taxon, nor taxa inhabiting the same island or island group, were well resolved. However, coarser patterns were detected. Amino acid sequence data were sufficient to segregate taxa inhabiting each of the following island groups: Dutch Leeward Islands, Puerto Rico, Cuba, Little Bahama Bank, and Grand Bahama Bank, with San Salvador and Turks and Caicos Islands grouping with the Grand Bahama Bank.

As with the nucleotide sequence data, all Delray specimens emerged in a single, highly supported clade that

also included the Cuban *C. tridentatum* and the two Fort Jefferson specimens. These results support an exclusively Cuban ancestry for all specimens in the clade. This clade was subdivided into two weakly supported subclades identical in composition to those based on nucleotide data, except that the two specimens from Fort Jefferson (*C. tridentatum costellata* and *C. sculptum*) were grouped together within the large clade. These two specimens shared a single tyrosine (TAT) to serine (TCG) substitution not present in any other *Cerion* studied.

It is interesting to note that *Cerion incanum* (Binney, 1851), from the Florida Keys, consistently grouped with the samples from Andros Island, Bahamas in both analyses, contradicting early hypotheses of a Cuban origin for this species (e.g., Binney, 1851: 153; Pilsbry, 1902: 213; 1907: 193; 1946: 162; Dall, 1905: 30).

DISCUSSION

The transplantation experiments conducted by Bartsch in the early 20th Century and subsequent, less well-documented intentional introductions by others (e.g., Krieger and Austin, 1975), are anathema to modern conservation biologists. Nevertheless, the survivors of Bartsch's diligently recorded experiments provide insights into the processes by which many of the numerous phenotypes within the genus *Cerion* (> 600 named species level taxa) may have arisen, and how they persist through time.

The original objective for the transplantations of propagules of *Cerion* from Andros Island to a number of the Florida Keys was to determine if their morphology would be altered over several generations by exposure to different environments (Bartsch, 1913). Years of careful measurement and segregation of multiple generations of progeny revealed that their morphology remained unaffected by habitat (Bartsch, 1920; Woodruff and Gould, 1987: 1023). However, in two instances the Andros Island *Cerion* hybridized with the native *Cerion incanum* to produce phenotypes that differed markedly from either parent species. This led Bartsch to redirect subsequent experiments to the production of hybrids. The majority of these efforts were focused on controlled, pairwise combinations of species (e.g., Bartsch, 1923a, 1924b), but some, such as those conducted on the parapets of Fort Jefferson, were simply the comingling of multiple species (Bartsch, 1924b).

The hypothesis that hurricanes play an important role in dispersing propagules of *Cerion* among neighboring islands has been widely accepted (e.g., Pilsbry, 1907; Mayr and Rosen, 1956; Clench, 1957). These infrequent, stochastic events are major factors determining biogeographic patterns within *Cerion*, and must have contributed to populating the Florida Keys and the islands of the Bahamas that had been completely submerged during Pleistocene interglacial high stands (Hearty et al., 1999). Subsequent introductions of propagules into the range of established populations of *Cerion* result in the formation of narrow hybrid zones in which the phenotypic variation exceeds that of either parent (Gould and Woodruff, 1986: 435–440), and that are characterized by the presence of unexpected alleles (hybrizymes) that do not occur in either parent taxon (Woodruff, 1989).

Gould and Woodruff (1990:78) showed that, whether the product of hurricane transport or human activity, such hybrid zones produce distinctive populations with sharply demarcated boundaries and are the results of "happenstances of history rather than forces of local adaptation." Such area effects are generally ephemeral, with both the genotype and phenotype of the hybrid subsumed into that of the numerically dominant parent taxon over time. Goodfriend and Gould (1996) documented that phenotypic traits in hybrid zones may persist for periods on the order of thousands to tens of thousands of years.

Very few of Bartsch's introductions survive to this day. The propagule of 500 adult *Cerion casablancae* introduced to Indian Key on June 1, 1912 (Bartsch, 1913: 130) has proliferated, and, in the continued absence of the native *Cerion incanum*, remains unchanged in its morphology, and presumably its genotype. On Bahia Honda Key, a surviving propagule of 55 *Cerion casablancae* hybridized with *Cerion incanum*, which reappeared on that Key between 1926 and 1931. The resulting hybrid phenotype and genotype continue to be assimilated into those of *C. incanum*. Based on allozyme studies, Woodruff and Gould (1987: 1040) calculated that "we may be unable to detect *C. casablancae* genes on Bahia Honda Key 350 years from now."

While these examples of Bartsch's transplantations can be expected to endure fates similar to those of hurricane introduced propagules, finding a parallel in nature for the Delray Beach colony is more difficult. Five Cuban taxa were introduced simultaneously into a small isolated area on the parapets of Fort Jefferson in June of 1924. The taxon *Cerion tridentatum costellata* was described based on specimens collected in 1941. This phenotype, not present in any of the five introduced Cuban taxa, was produced in 17 years, roughly 3–5 generations, based on estimates of a generation time of 4–5 years (Woodruff, 1978: 229). A propagule from Fort Jefferson of unknown size and composition (Pilsbry [1946] reported that *C. chrysalis fastigatum*, *C. sculptum marielinum*, *Cerion tridentatum* [rare] and *Cerion tridentatum costellata* were all present on Fort Jefferson in 1941) was introduced to the "McGinty lawn" in Boynton Beach in the late 1940s, and possibly admixed with one or more propagules of other *Cerion* from Florida and/ or Andros Island. After 60 + years, this population has expanded geographically, and is estimated to exceed 10^5 individuals. Specimens are fairly uniform in morphology (Figures 1, 2; Harasewych and Strauss, 2006: figs. 1–8), with the exception that some

are white and others are mottled. Limited genetic sampling (n = 8) indieates the presence of mitoehondrial genes from two (*C. tridentatum* and *C. sculptum mariclinum*) of the five speeies originally introdueed onto the parapets at Fort Jefferson in a 3:1 ratio that does not eorrelate with the presenee of mottling. The possibility of as yet undeteeted rare alleles from other taxa cannot be ruled out. The Delray Beaeh colony of *Cerion tridentatum costellata* is more than 100 km distant from the nearest neighboring population of *Cerion*. Thus, this "happenstance of history" has plaeed a newly formed hybrid propagule in an area far removed from either parent population. Rather than being subsumed, it will eontinue to evolve in isolation for the foreseeable future and provides a unique opportunity to study the origins and persistenee of genetic diversity within the genus *Cerion*.

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Mexistrophia, a new genus of Cerionidae from Mexico (Gastropoda: Pulmonata: Urocoptoidea)

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ABSTRACT

Mexistrophia new genus and three new species of the landsnail family Cerionidae, *Mexistrophia reticulata* new species, *M. obsoleta* new species, *M. inexpectata* new species, are described from northeastern México. The genus is characterized by the absence of lamella or other barriers within the shell. The genus is diagnosed by soft anatomical features as well as shell characteristics. The known distribution of *Mexistrophia* is confined to higher elevations at 2000–2600 meters in the Sierra Madre Oriental in the states of Nuevo León, Querétaro and Hidalgo, where it inhabits cool temperate conifer forests that are subject to seasonal frosts and occasional freezes. Its distribution is disjunct geographically and ecologically from that of *Cerion*, which is confined to the tropical Caribbean region at very low elevations.

Additional keywords: Landsnails, biodiversity, endemism

INTRODUCTION

A prevailing misconeeption in molluscan biogeography is that the land snail family Cerionidae is an autoehthonous West Indian element. *Cerion*, the only extant genus reeognized in the family, has undergone extensive speeiation, but has never sueeessfully eolonized the mainland, even though on at least two occasions species became established in Florida, onee in the Oligocene (Dall, 1890), and once by the more reeently derived *Cerion incanum* (Binney, 1857). Roth and Hartman (1998) report a probable eerionid, *Cerion archerontis*, from the Uppermost Cretaceous of Montana. However, the type specimen is a fragmented and flattened fossil that defies clear taxonomie characterization.

During the last forty years, while conducting field work in Mexico, oceasionally I collected peculiar cylindric-conical snails that I identified tentatively as "*Cerion*". They were found in habitats uncharacteristic of *Cerion*. They were set aside among undetermined "Urocoptidae" until now. Anatomieal and conchological examinations reveal that they are Cerionidae, but that they differ from *Cerion* as a separate genus. Three new species are described.

Abbreviations and Text Conventions: The following symbols are used in the illustrations of anatomieal struetures: **albl,** albumen gland; **atr,** atrium; **app,** appendix; **div,** divertieulum; **epi,** epiphallus; **fovi,** free oviduet; **ovid,** oviduet; **pen,** penis; **prm,** penis retraetor musele: **pro,** prostate; **rom,** right oeular retraetor musele; **spd,** spermathecal duet; **spr,** spermatheea; **vag,** vagina; **vas,** vas deferens; **vrm,** vaginal retraetor musele; Institutional abbreviations: CNMO: Coleeión Naeional de Moluseos, Mexico; UF: Florida Museum of Natural History, Gainesville.

SYSTEMATICS

Mexistrophia new genus

Type Species: *Mexistrophia reticulata* new speeies.

Description: Shell small, 10–13 mm length. Shell pupiform, with a low dome-shaped apex. Protoeoneh whorls smooth and do not eonspieuously rise above following whorl. Peristome thiekened, but only slightly so, not refleeted, ineomplete aeross parietal wall. Outer lip and eolumellar lip eonnected by thin parietal eallus. Outer surface seulptured with fine axial thread-riblets. Internal axis broad and hollow in upper whorls of dome-like apex, then narrowing and beeoming narrowly perforate or solid in last two or three whorls. Internal barrier of lamellae or dentieles laeking at all growth stages (in eontrast with *Cerion*.)

Anatomy: General anatomical states typieally Cerionidae. Short foot laeking a suprapedal groove. Plain lung, with unbranched pulmonary vein. Kidney short, with very short ureter near the end. Seeondary ureter absent.

Reproductive system typieally cerionid. Genital atrium moderately long and capaeious. Epiphallus poorly differentiated from vas deferens. Epiphallus + vas deferens form very long loop that extends alongside oviduet-prostate. Penis consists of two parts. Epiphallus entering middle of penis. Penis ending in blind diverticulum distal

to epiphallus. Penis retractor muscle inserts on apex of diverticulum. Right ocular retractor muscle passes mesad to genitalia and attaches to right pedal retractor muscle. Spermathecal duct very long, with very long appendix, or lacking an appendix. Spermathecal duct unites with free oviduct to form distinct vagina. Free oviduct stout and slightly longer than vagina. Stout vaginal retractor muscle originates on right ocular retractor muscle and inserts on vagina (Figures 24–25).

Radula of *Mexistrophia* is typical Cerionidae with nearly flat horizontal tooth rows that do not curve upward near margins. Central tooth tricuspid. Lateral and marginal teeth bicuspid with large mesocone and small ectocone. Mesocone of marginal teeth long, extending beyond base of tooth. Laterals and marginals lacking entocones.

Habitat and Distribution: *Mexistrophia* are ground-dwelling snails that are found in eastern Mexico in cool temperate coniferous forests at high elevations.

Etymology: *Mexistrophia* (f.). The genus name is taken from *Mexi-*, Mexico, and *strophia*, Gr. **στροφέ**, a turning point, such as an axis. *Strophia* Albers, 1850 is an earlier generic name that was widely used for *Cerion* (not *Strophia* Meigen, 1832, Lepidoptera).

Mexistrophia reticulata new species

(Figures 1–6, 20, 22, 27, 28, Table 1)

Diagnosis: Pupiform shell, moderately robust, about 9–13 mm long. Conspicuous white peristome lacking noticeable callus reinforcing it internally. Sculpture consisting of thread-riblets, with upper ends that weakly crenulate the suture. Spermathecal duct with long appendix.

Description: Shell (Figures 1–6). Shell pupiform. Spire cylindrical, relatively slender, with low domed-shaped apex. Shell wall opaque. Ground color light brown mottled with lighter irregular-shaped spots and streaks that form reticulated pattern. White streaks tend most conspicuous on upper ends of ribs. Peristome and adjacent interior of aperture white. Deeper within, inner wall and axis rust-colored. Shell 10.5–13.2 mm long, 3.9–4.4 mm wide, and 0.31–0.38 times as wide as long. Shell contains 8.0–9.2 whorls separated by weakly impressed suture. Protoconch consisting of two smooth whorls slightly elevated above following whorls. Following whorls sculptured with numerous oblique thread-riblets strongest on apical whorl, but nearly equally developed on spire. Riblets strongest below suture and weakly crenulate suture. Umbilicus imperforate or narrowly rimate. Thick peristome weakly reflected and discontinuous across parietal wall, where it is replaced by thin glaze. Aperture ovate, slightly higher than wide, 0.28–0.33 times shell length, and 0.67–0.80 times shell width. Aperture slightly prosocline in lateral profile (Figure 5). Axis conspicuously enlarged in apical whorls. Cylindric part of shell axis slightly sinuous, much narrower, and narrowly perforate or solid by last whorl (Figure 6). (Measurements based on the holotype and twelve paratypes are given in Table 1.)

Anatomy: Reproductive anatomy (Figures 20–22) (Five specimens examined (UF 211129): Genital atrium (**atr**) moderately long and capacious. Right ocular retractor a narrow slip of muscle that passes mesad to lower genitalia, attaching to vagina in conjunction with vaginal retractor muscle. Stout penis (pen) bulbous, consisting of two nearly equal sections. Distal section forming globose, blind diverticulum (div). Short penis retractor muscle (prm) originating on inner wall of lung and inserting on end of diverticulum. Epiphallus (epi) entering middle of penis at base of diverticulum. Epiphallus moderately stout at union with penis, but gradually grading into very long vas deferens. Epiphallus lined internally with simple longitudinal columns. Spermatheca (spr) large and elliptical, resting against dorsal side of oviduct at base of albumen gland. Spermathecal duct (spd) stout, moderately long, enlarged at base where it is muscular and weakly convoluted. Duct bearing very long appendix (app) about as long as spermathecal duct. End of appendix extending to upper end of albumen gland. Spermathecal duct uniting with free oviduct (fovi) to form short but distinct vagina (vag). Free oviduct relatively stout and slightly longer than vagina. Heavy slip of muscle that is a branch of right pedal retractor inserting on vagina to form vaginal retractor muscle (vrm) (Figures 21–22).

Radula (Figures 27–28). Two specimens examined (UF 445301). Radular formula 14-1-14. Transverse tooth rows nearly flat, not curving upward at ends. Transition from lateral teeth to marginal teeth not clearly differentiated morphologically. Eight lateral teeth and 6 marginal teeth present in each half-row. Lateral teeth rising slightly, and marginal teeth becoming nearly horizontal. Central tooth trapezoidal with indented dorsal edge, 18 µm wide and 20 µm high. Central tooth with large lanceolate mesocone, 15 µm long, extending to base of tooth. Mesocone flanked on each side by short acuminate ectocone. Lateral teeth with long, slender mesocone overlaping tooth below, and small ectocone. Marginal teeth with long mesocone and small ectocone.

Type Locality: A talus slope 1.0 km east of Pinal de Amoles, Querétaro State, Mexico, 21.15° N, 99.64° W, 2150 m alt.

Type Material: Holotype: UF 211128, collected 25 July, 1993 by Fred G. Thompson and Elizabeth L. Mihalcik; Paratypes: UF 435013 (30), CNMO 3379 (5), all from type locality.

Other Material Examined: UF 211129; type locality. Specimens preserved in 75% ETOH.

Habitat: The dominant vegetation in the area consists of pine forests with scattered small oak trees

Figures 1–19. New species of *Mexistrophia*. **1–6.** *Mexistrophia reticulata* new species. **1.** Holotype (UF 211128). **2–6.** Paratypes (UF 43513). **7–10.** *Mexistrophia obsoleta* new species. **7.** Holotype (UF 34296). **8–10.** Paratypes (UF 435015). **11–19.** *Mexistrophia inexpectata* new species. **11.** Holotype (UF 226461). **12–19.** Paratypes (UF 435014). Seale bar for Figure 1 applies to Figures 1–6; for Figure 7 to Figures 7–10; for Figure 11 to Figures 11–19.

(*Quercus* sp.). Snails were found among grasses, mosses and *Sedum* growing among limestone cobbles.

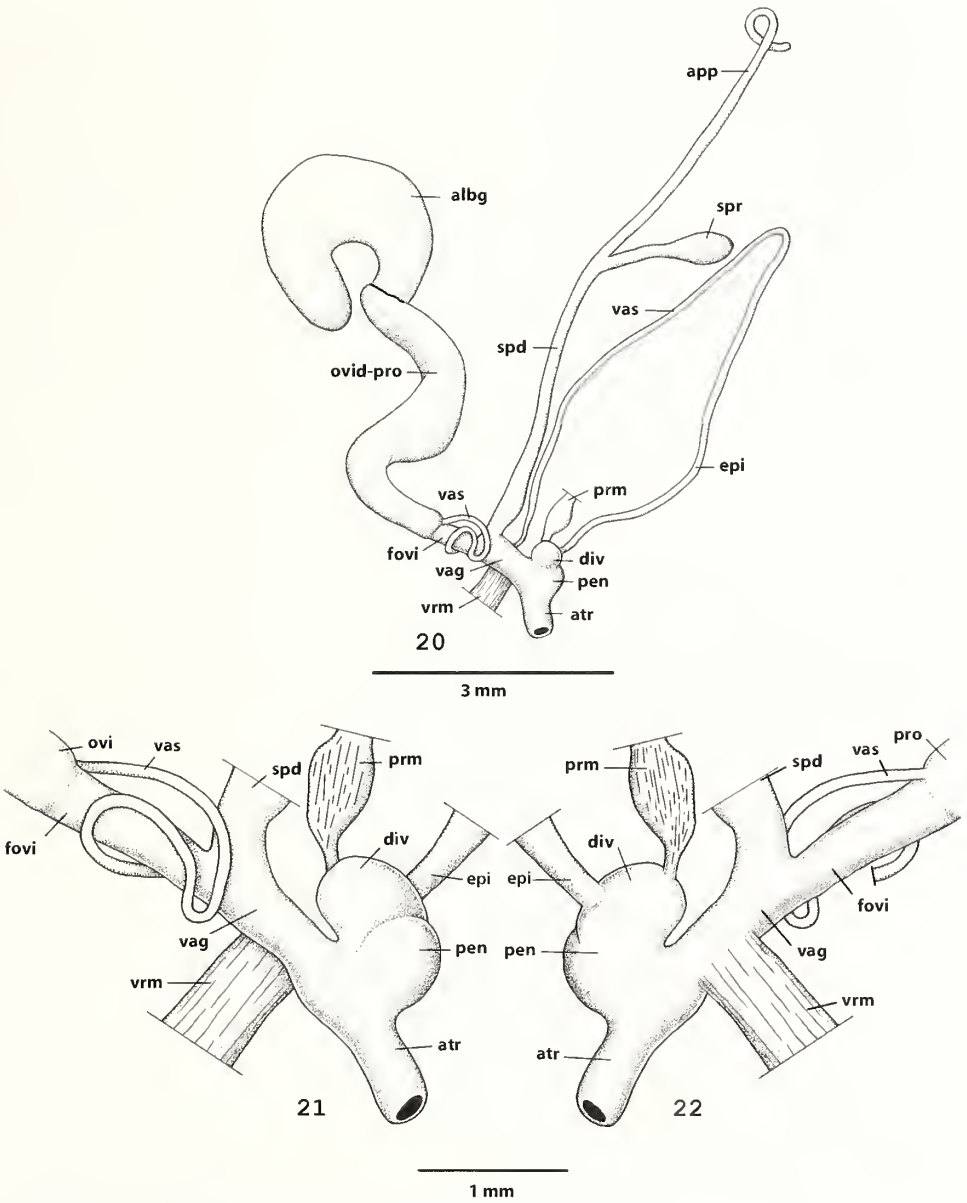
Distribution: Querétaro State, Mexico (known only from the type locality.)

Remarks: For meristie comparisons with other species see *Mexistrophia inexpectata* new species below.

Etymology: The speeies name *reticulata* (Latin) alludes to the reticulated color pattern of the shell.

Table 1. *Mexistrophia reticulata* new species. Measurements in mm of the holotype (UF 211128) and 12 paratypes (UF 435013) selected to show variation. SL = standard length, SW = standard width, ApH = aperture height, ApW = aperture width, Wh = whorls.

	SL	SW	ApH	ApW	Wh	SW/SL	ApH/SL	ApW/SW
Holotype	11.0	3.9	3.6	3.0	8.9	0.35	0.33	0.77
Paratypes								
Min	10.5	3.9	3.2	2.8	8.0	0.31	0.28	0.67
Max	13.2	4.4	3.8	3.2	9.2	0.38	0.33	0.80
Avg	11.55	4.04	3.55	2.98	8.65	0.35	0.31	0.74
STD	0.88	0.14	0.19	0.17	0.41	0.02	0.02	0.03



Figures 20–22. *Mexistrophia reticulata* new species, reproductive anatomy (UF 211129).

Mexistrophia obsoleta new species

Diagnosis: Distinguished by obese pupiform shape, obsolescent color pattern, and sculpture in which upper ends of ribs do not crenulate suture and ribs become obsolete or are absent on lower two whorls. Peristome white, relatively narrow, lacking noticeable callus within.

Description: Shell (Figures 7–10) obese-pupiform, squat cylindrical spire with low domed-shaped apex with protoconch barely elevated above following whorl. Shell wall opaque. Ground color light tan with obsolescent mottling with lighter irregular spots and streaks that do not form distinct pattern. White streaks most conspicuous on ribs. Peristome and adjacent interior of aperture white. Deeper within aperture, inner wall and axis very light rust-colored. Shell 10.5–12.3 mm long, 4.2–4.8 mm wide, and 0.35–0.41 times as wide as long. Shell contains 8.2–9.1 whorls separated by weakly impressed suture. Protoconch with two smooth whorls. Following whorls sculptured with numerous, relatively strong, oblique thread-riblets nearly equally developed on apex and earlier whorls of cylinder, becoming obsolete on lower two whorls. Upper ends of riblets do not crenulate suture. Umbilicus imperforate or narrowly rimate. Peristome relatively thin, weakly reflected, and discontinuous across parietal wall, where it is replaced by thin callus. Ovate aperture slightly higher than wide, 0.26–0.32 times shell length, and 0.63–0.72 times shell width. Aperture slightly prosocline in lateral profile, not noticeably thickened within. Axis enlarged in apical whorls (Figure 10). In cylindric part of shell axis nearly straight, narrower, becoming narrowly perforate or solid by last whorl. (Measurements based on the holotype and ten paratypes are given in Table 2.)

Anatomy: Unknown.

Type Locality: A limestone ravine 15.8 km by road southwest of Pinal de Amoles, Querétaro State, Mexico (21.15° N, 99.65° W), 2585 m alt.

Type Material: Holotype UF 34298; collected 27 September, 1970 by Fred G. Thompson; Paratypes UF 435015 (25), CNMO 3373(5); all from type locality.

Distribution: Querétaro State, known from the type locality and a nearby locality 2 km ENE of Pinal de Amoles, 2140 m alt. (UF 268262).

Remarks: For meristic comparisons with other species see *Mexistrophia inexpectata* new species, below.

Etymology: The species name *obsoleta* (Latin) refers to the barely discernable reticulated color pattern on the shell, and its sculpture, which becomes obsolete on the last two whorls.

Mexistrophia inexpectata new species

Diagnosis: Relatively slender, pupiform shell with nine or more whorls. Sculpture nearly uniform over shell surface, consisting of fine oblique thread-riblets. Peristome narrowly reflected and reinforced internally by thick callus. Spermathecal duct lacking an appendix.

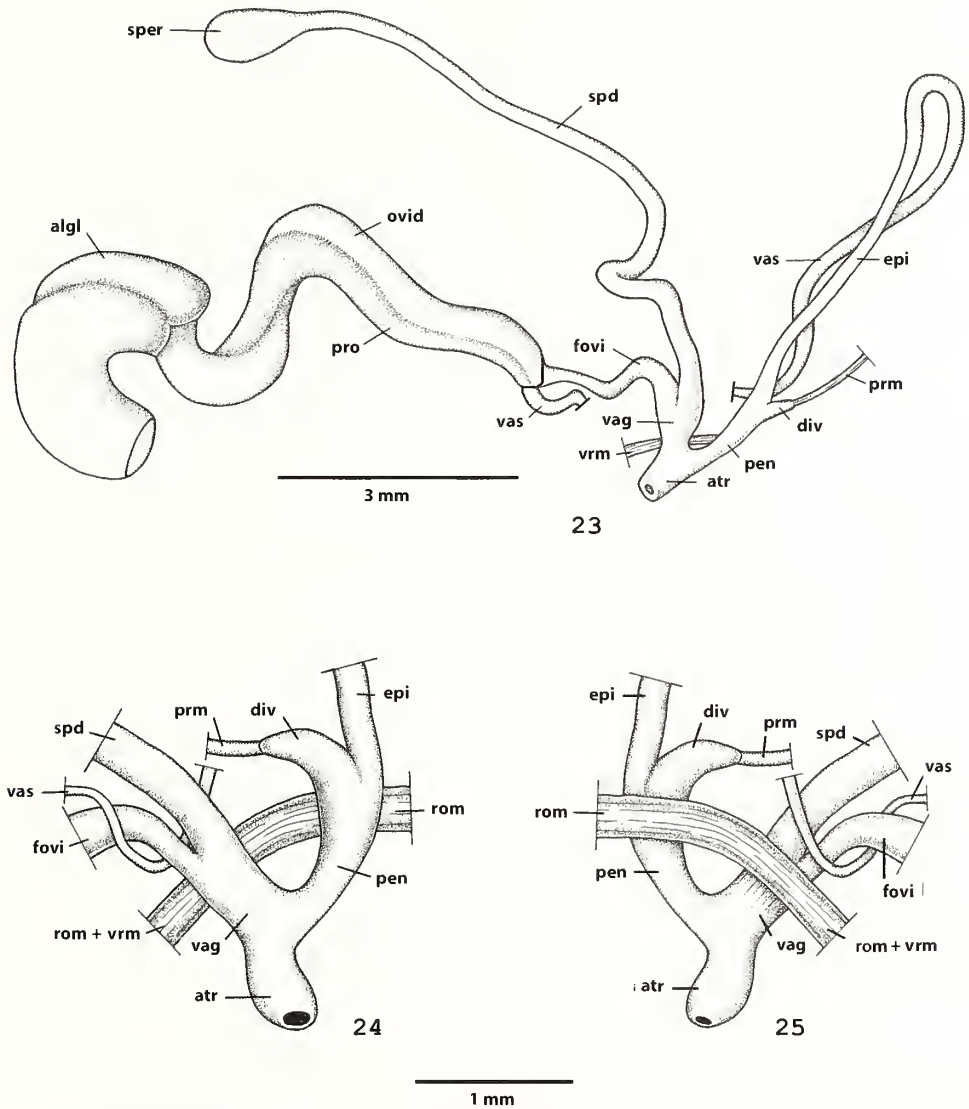
Description: Shell (Figures 11–19) pupiform. Cylindrical spire bearing low domed-shaped apex. Shell wall opaque or weakly translucent. Ground color light brown with sparse lighter irregular spots and streaks. White streaks most conspicuous on upper ends of ribs. Peristome and adjacent interior of aperture white. Deeper within inner wall and axis rust-colored. Shell 9.8 12.4 mm long, 3.3–3.5 mm wide, and 0.38–0.35 times as wide as long, with 9.1–11.0 whorls. Suture weakly impressed. Protoconch with two smooth whorls slightly elevated above following whorls. Following whorls sculptured with numerous oblique thread-riblets nearly equally developed over shell surface. Riblets do not crenulate suture. Umbilicus imperforate or narrowly rimate. Thick peristome weakly reflected and discontinuous across parietal wall, where it is replaced by thin glaze. Peristome reinforced internally by thick callus. Aperture ovate, slightly higher than wide, 0.24–0.37 times shell length, and 0.69–0.76 times shell width, slightly prosocline, nearly vertical in lateral profile (Figure 18). Axis conspicuously enlarged in apical whorls, straight in cylindric part of shell, very narrow, becoming narrowly perforate or solid by last two whorls (Figure 19). (Measurements based on the holotype and ten paratypes are given in Table 3.)

Table 2. *Mexistrophia obsoleta* new species. Measurements in mm of the holotype (UF 34298) and 10 paratypes (UF 435015) selected to show variation. SL = standard length, SW = standard width, ApH = aperture height, ApW = aperture width, Wh = whorls.

	SL	SW	ApH	ApW	Wh	SW/SL	ApH/SL	ApW/SW
Holotype	11.2	4.2	3.4	3.1	8.3	0.38	0.29	0.81
Paratypes								
min	10.5	4.2	3.2	2.7	8.2	0.35	0.26	0.63
max	12.3	4.8	3.5	3.4	9.1	0.41	0.32	0.71
avg	11.38	4.36	3.33	2.59	8.52	0.38	0.29	0.68
STD	0.56	0.20	0.11	0.18	0.30	0.02	0.02	0.05

Table 3. *Mexistrophia inexpectata* new species. Measurements in mm of the holotype (UF 226407) and 10 paratypes (UF 485014) selected to show variation. SL = standard length, SW = standard width, ApH = aperture height, ApW = aperture width, Wh = whorls.

	SL	SW	ApH	ApW	Wh	SW/SL	ApH/SL	ApW/SW
Holotype	11.4	3.5	3.0	2.4	9.2	0.31	0.26	0.69
Paratypes								
Min	9.8	3.3	2.7	2.3	9.1	0.28	0.24	0.69
Max	12.4	3.6	3.0	2.6	11.0	0.35	0.27	0.76
Avg	10.87	3.42	2.84	2.46	9.71	0.32	0.26	0.72
STD	0.70	0.10	0.17	0.09	0.51	0.02	0.01	0.02



Figures 23–25. *Mexistrophia inexpectata* new species, reproductive anatomy (UF 226408).

Anatomy: Reproductive anatomy (Figures 23–25) (Five specimens examined (UF 226408): Genital atrium (atr) moderately long and stocky. Penis (pen) moderately long and slender, ending in slender, short, blind diverticulum (div). Penis lined internally with six longitudinal columns, lacks verge or stimulator. Penis retractor muscle (prm) long and slender, originating on inner lung wall and inserting on diverticulum end. Right ocular retractor

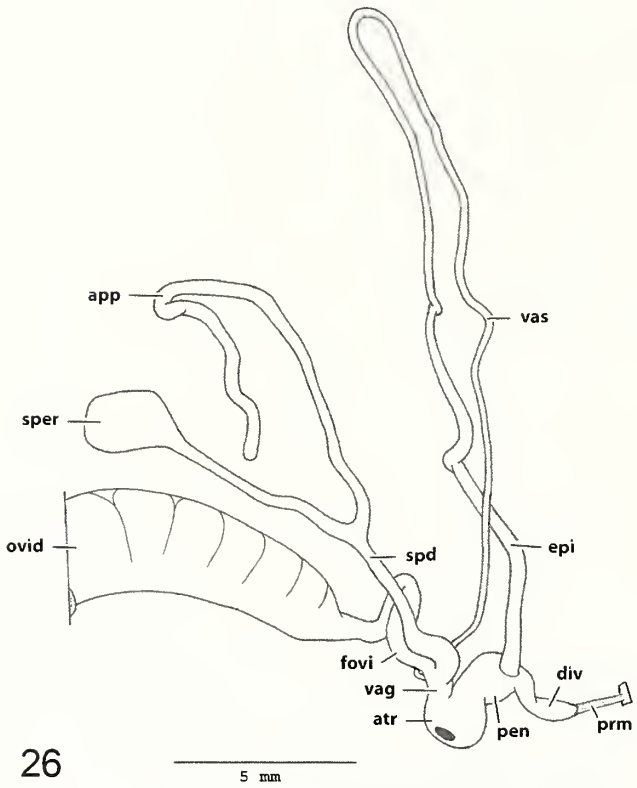


Figure 26. *Cerion uva* (Linnaeus, 1758). Reproductive anatomy (UF 336946).

muscle (rom) passing mesad to genital system and inserting into right pedal retractor muscle, attached to vagina (vag) by short slips of muscle (Figure 25). Epiphallus (epi) entering the penis (pen) shortly below diverticulum, long, stout, and poorly differentiated from vas deferens (vas). Elliptical spermatheca (sper) resting against side of oviduct-prostate at base of albumen gland. Spermathecal duct (spd) relatively stout and lacking appendix. Duct uniting with free oviduct (fovi) to form short but well developed vagina (vag). Free oviduct short but stocky, about as long as combined length of vagina + genital atrium.

Radula (Figures 29–30) (Two specimens examined, UF 226408): Radular ribbon 0.55 mm wide by 1.34 mm long. Radular formula 18-1-18. Transverse tooth rows horizontal, nearly straight, not curving upward at margins. Eighteen lateral + marginal teeth present. Lateral teeth transition without morphological distinction into marginal teeth. Central tooth as wide as adjacent lateral teeth, 16 µm wide, trapezoidal, tricuspid. Mesocone acuminate, extending beyond tooth base, bordered on each side by short acuminate ectocone. All seven lateral teeth bicuspid with large acuminate mesocone and smaller acuminate ectocone. Marginal teeth with large lanceolate mesocone and single acuminate ectocone.

Type Locality: A west-facing hillside on a limestone exposure, 0.5 km north of El Refugio, Nuevo León, Mexico (23.921° N, 99.719° W), 2360 m alt. The type locality is in a grassy open "piñon" (pine) forest with scattered agave and small oaks. Snails were collected from among and under flags of limestone.

Type Material: Holotype UF 226407; collected 24 July, 1994 by Fred G. Thompson, Elizabeth Mihalcik, Grady Taylor, and Val J. Roessling; Paratypes UF 435014 (85), CNMO 3371 (10); same data as the holotype; UF 267253 (33); collected January, 1996 by Val J. Roessling; all from type locality.

Distribution: Nuevo León State, known only from the type locality.

Etymology: The species name *inexpectatus* is from the Latin and alludes to the fact that the reproductive system differs from what I anticipated before dissecting the species.

Remarks: Shell measurements of the three species of *Mexistrophia* may be compared as in Table 4. *Mexistrophia inexpectata* is separated from *M. reticulata* and *M. obsoleta* by its slender size and by its larger number of whorls.

ADDITIONAL *MEXISTROPHIA*

Specimens of *Mexistrophia* are available from the localities below. They differ from the new species described above by size, obesity, and whorl count enough to suggest that they represent different species. Their taxonomic status remains undetermined because only shell samples are available for study. These samples indicate that the genus is widespread in northeastern Mexico.

Nuevo León: 1.7 km N El Refugio, 18 km. S of Zaragosa; (UF 258407), collected 4 November, 1995 by Val J. Roesling.

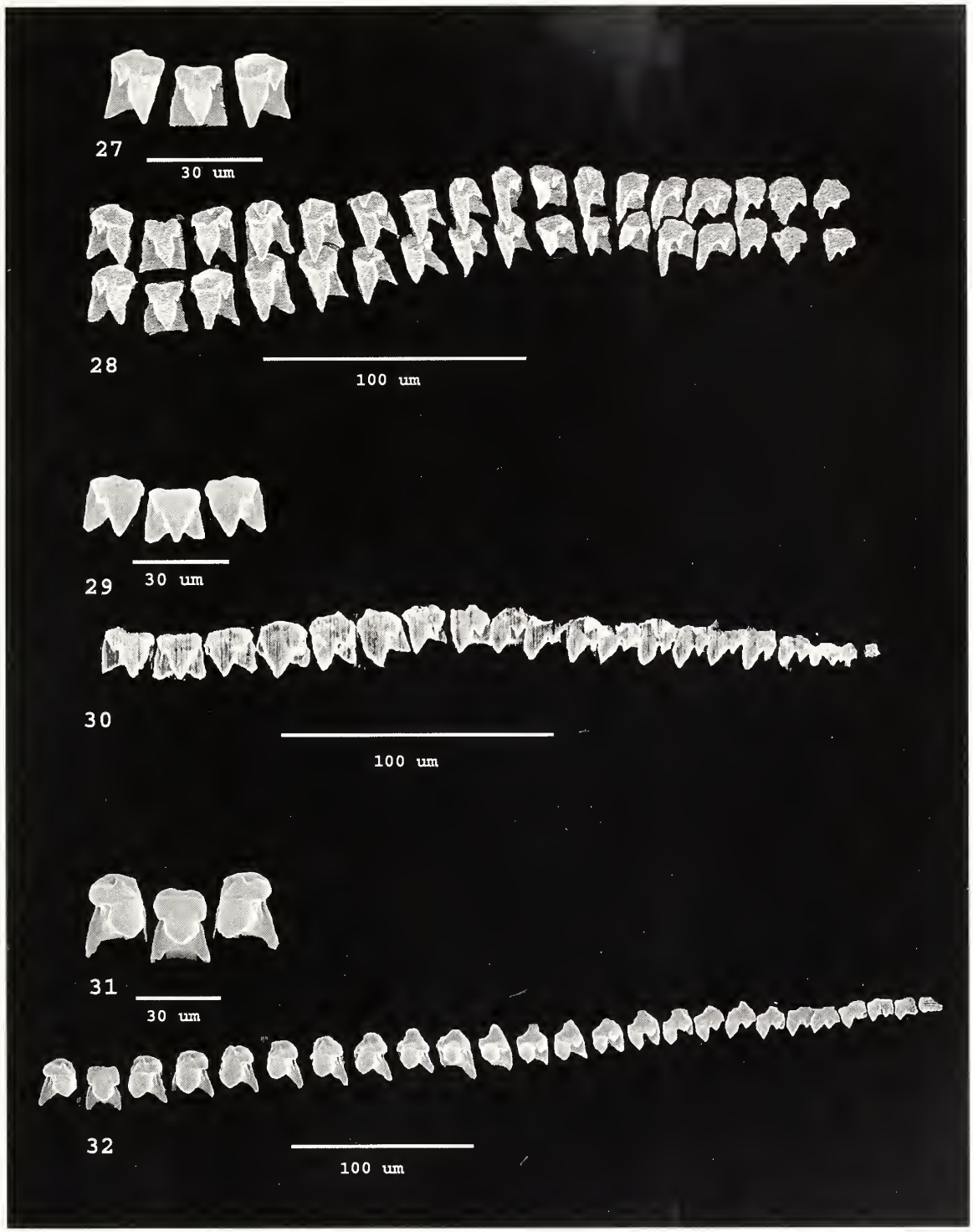
Hidalgo: Ixmiquilpan (20.483° N, 99.233° W) (UF 179719); leg. Gonzalo Halfter, collected 6 March, 1960.

Qeurétaro: 14 km NE of San Juaquín, turn-off from Mexico Highway 120 (18.756° N, 96.189° W), 2400 m alt. (UF 244942); collected by Grady H. Taylor, 8 September 1978.

GEOGRAPHIC DISTRIBUTION OF THE FAMILY CERIONIDAE

(Figures 33–34)

Mexistrophia is found in eastern Mexico over a north–south linear distance of about 400 km, and inland by about 200 km west of the Gulf of Mexico (Figure 33). It is known from the states of Nuevo León, Querétaro, and Hidalgo, at elevations between 2150–2585 meters. This is about 1600 km west of the nearest locality from where *Cerion* has been reported in the West Indies (Figure 34). *Cerion* is strictly a West Indian genus found in Cuba, Bahamas Islands, Hispaniola, Puerto Rico, St. Croix, and the Cayman Islands (Fahy, 1996). A single



Figures 27–32. *Mexistrophia* and *Cerion uva*, SEM micrographs or radula. **27–28.** *Mexistrophia reticulata* new species (UF 445301). **27.** Central and adjaeent lateral teeth. **28.** Hemi-sections of two horizontal teeth rows. **9–30.** *Mexistrophia inexpectata* new species (UF 226408). **29.** Central and lateral teeth. **30.** Hemi-section of a horizontal tooth row. **31–32.** *Cerion uva* (UF 249358). **31.** Central and adjacent lateral teeth. **32.** Hemi-seetion of a horizontal tooth row.

Table 4. Comparisons of measurements (mm) and meristic counts among the three new species of *Mexistrophia* described in this article.

	M. reticulata	*M. obsoleta*	*M. inexpectata*
SL	10.5–13.2	10.5–12.3	9.8–12.4
SW	3.9–4.4	4.2–4.8	3.3–3.6
ApH	3.2–3.8	3.2–3.5	2.7–3.0
ApW	2.8–3.2	2.7–3.4	2.3–2.6
Whorls	8.0–9.2	8.2–9.1	9.1–11.0
SW/SL	0.31–0.38	0.35–0.41	0.28–0.35
ApH/SL	0.28–0.33	0.26–0.32	0.24–0.27
ApW/SW	0.67–0.80	0.63–0.72	0.69–0.76

species, *C. uva* (Linnaeus, 1758), occurs on the Dutch Leeward Islands. A single species, *C. incanum* (A. Binney, 1857), occurs naturally on the mainland in extreme southeastern Florida. No species of *Cerion* has been found in suitable coastal habitats in eastern Mexico or Central America, although during the last two centuries experienced collectors searched such habitats for non-marine mollusks at numerous localities.

ECOLOGICAL DEPLOYMENT OF *MEXISTROPHIA*

The ecological deployment of *Mexistrophia* contrasts strongly with the ecological distribution of West Indian Cerionidae. Nearly all West Indian Cerionidae are found at very low elevations, of only a few meters to tens of meters. Generally they occur at just a few meters to a few kilometers from the nearest shoreline among tropical vegetative associations.

In striking contrast species of *Mexistrophia* occur at elevations of greater than 2000 meters, and are found inland at more than 200 kilometers from the Gulf of Mexico. They occur in cool mesic or submesic temperate coniferous forests. Winter frosts and occasional freezes are normal at localities from where the genus is known.

COMPARISONS OF *MEXISTROPHIA* WITH *CERION*

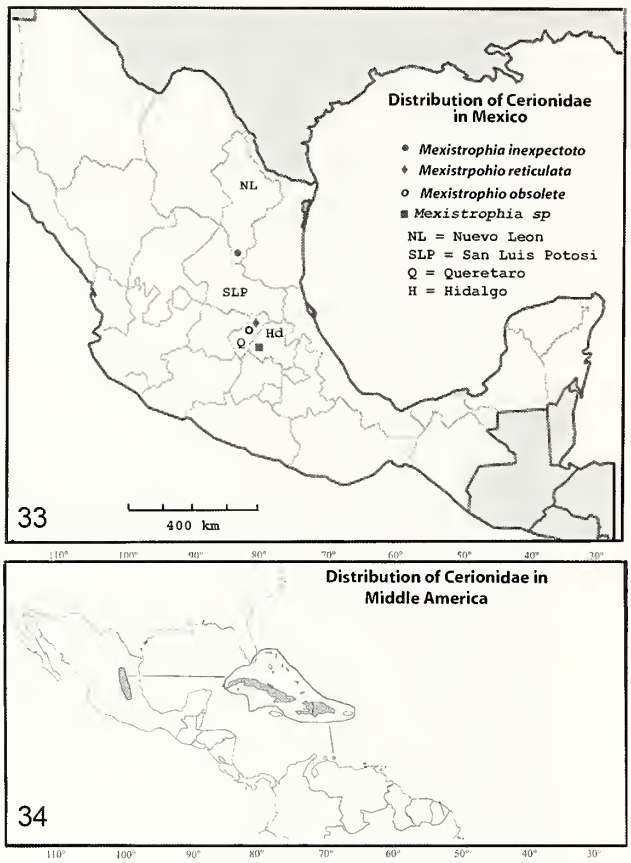
The anatomy of the *Cerion* remains poorly studies. Anatomical information is available for the following species:

Cerion (*Strophiops*) *incanum* (Binney, 1857): Pilsbry, 1902: 176–178 [radula]; Pilsbry, 1946: 159–161 [reproductive anatomy].

Cerion (*Strophiops*) *glans* (Kuster, 1847): Richter, 1926: 277–342 [reproductive anatomy]; Jaenicke, 1933.

Cerion (*Strophiops*) *mumia chrysalis* (Férussac): Pilsbry, 1902: 176–178 [reproductive anatomy].

Cerion striatellum (Guerin-Manneville, 1829): Baker, 1961: 33–34 [lung, reproductive anatomy].



Figures 33. Distribution of Cerionidae in Mexico. **34.** Distribution of Cerionidae in Middle America.

Cerion (*Cerion*) *uva* (Linnaeus, 1776): Baker, 1961: 34–35); Thompson, this report; Netherlands Antilles, Curaçao, beach at Christenffel Nationl Park (UF 336946).

CHARACTERIZATION OF THE CERIONIDAE

The available data, although limited, allow the Cerionidae to be characterized as follows. The foot is short and lacks a pedal groove. The ureter is confined to the anterior end of the kidney. A secondary ureter is absent. The plain lung has an unbranched pulmonary artery. The reproductive anatomy has a blind diverticulum on the end of the penis (Figure 26). The right ocular retractor is a narrow slip of muscle that passes mesad to the lower genitalia and unites with the right pedal retractor muscle. It is attached to the vagina in conjunction with the vaginal retractor muscle. The penis retractor muscle inserts on the apex of the diverticulum. The epiphallus enters the penis at the base of the diverticulum. The vagina is moderately long. The spermathecal duct bears a very long appendix. The jaw is finely ribbed. The radula differs from other urocoptoid families as follow. The transverse tooth rows are nearly horizontal and are not curved upward at the margins. The central

tooth is trieuspid with a large mezocone bordered on eaeh side by a small eetoeone. The lateral teeth and the marginal teeth are bicuspid with a large mesoeone and a smaller eetoeone. The mesocone is elongate and extends beyond the base of the tooth. Entocones are absent.

Remarks: *Mexistrophia reticulata* is typical of the Cerionidae in its anatomieal states. *Mexistrophia inexpectata* departs from the general morphology of *Cerion* by laeking a diverticulum on the spermatheeal duct. This trait is considered a derived state, beeause the presence of a divertieulum among stylommatophoran families is so widespread that its presence must be considered plesiomorphic (Nordsieck, 2007). The taxonomie signifieanee of the absenee of a diverticulum in *M. inexpectata* remains to be determined beeause the loss of a diverticulum within families, subfamilies, and genera occurred in several oeeasions.

Mexistrophia differs in shell features from *Cerion* by laeking internal lamellae and dentieles at all stages of growth. Juvenile of many *Cerion* speeies have 2–5 denticles within the early whorls in addition to an axial lamella and a parietal lamella or dentiele in the adult stage. A eomparison of *Mexostrophia* to subgenerie groups within *Cerion* shows no elose relationship to any subgenus.

Cerion contains various extant subgenera and a single fossil subgenus, *Eustrophia* Dall 1890. The extant subgenera are found on the Bahamas Islands, the Greater Antilles except Jamaiea, St. Croix and the Dutch Leeward Islands. The subgenera differ by the location of the axial lamella and the parietal lamella or denticles. All of the subgenera except the fossil *Eustrophia* have a columellar lamella and a parietal lamella or tooth that is visible within the aperture. *Eustrophia* ineludes a single species, *Cerion* (*Eustrophia*) *anadonta* (Dall, 1890). It is a large, robust, poorly known fossil from the Oligoeene Silex beds of Florida. It has been reported from several loealities in the Upper Oligoeene–Lower Mioeene of Florida (Mansfield, 1937), but no information is available eoncerning the internal morphology of the shell. It was described originally as lacking an axial lamella and a parietal tooth. However, the holotype (USNM 111972) has a parietal tooth (Harasewych, 2009). The absence of an internally confined axial lamella is not confirmed because no speeimen has been disseeted for examination of this trait.

No close relationship between *Mexistrophia* and a particular subgenus of *Cerion* is evident. A close relationship between *Mexistrophia* and *Eustrophia* is not plausible because of their general dissimilarities. To apply a generic name based on an imperfectly known fossil speeies to a modern group is of very dubious value.

Roth and Hartman (1998) report a probable speeies of *Cerion* from the uppermost Cretaceous Hell Creek Formation of Montana. *Cerion acherantia* Roth and Hartman, 1998 is based on a fractured and eompressed shell that defies clear characterization. The identity of this species as a eerionid is to some extent supported by the discovery of modern Cerionidae in Mexico.

Speculation in the literature related Cerionidae to the Clausiliidae and other families placed in the Mesurethra (Emberton et al., 1990). Uit de Weerd (2008) demonstrated that the Cerionidae belong in the Urocoptoidea, and that they are most elosely related to the Holospiridae on the basis of 28S rRNA sequence data. If Cerionidae are recognized as a distinet family, the Holospiridae and the Eueolodiidae must also be recognized as separate families because their 28S rRNA, soft anatomies, and basie shell structures differ from Urocoptidae as much as or greater than do the Cerionidae.

ACKNOWLEDGMENTS

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New Cretaceous turbiniform vetigastropods (Gastropoda) from the Pacific slope of North America

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ABSTRACT

Seven new species of warm-temperate, shallow-marine turbiniform vetigastropods are described from Cretaceous strata in the region extending from Vancouver Island, British Columbia, to northern Baja California, Mexico. The chilodontine *Agathodonta luegerti* new species (latest Santonian) is the first confirmed species of this extant genus in the Western Hemisphere. The calliotropine *Cidarina grahami* new species (middle Campanian) is the earliest record of this extant genus. The eolloniines *Afrollonia elderensis* new species (late Albian) and *Antillocollonia bos* new species (Turonian) are the earliest records of these extinct genera in Western Hemisphere. The tegaline *Tegula daileyi* new species (late Campanian) is one of the few known Campanian species of this extant genus. The margaritines *Pupillaria encina* new species and *Pupillaria lomana* new species (both of which are late Campanian to possibly early Maastrichtian in age) are the earliest records of this extant genus.

During the course of this study, it was discovered that the nododelphinulid *Trochacanthus wallalense* (White, 1885) (late Campanian to early late Maastrichtian) is the senior synonym of *T. pacificus* Squires and Saul, 2001. White's species is the only known occurrence of this extinct genus in the Western Hemisphere.

Additional keywords: Amberleyoidea, Seguenzioidea, Turbinoidea

INTRODUCTION

This study concerns turbiniform vetigastropods from shallow-marine Cretaceous rocks in the region extending from Vancouver Island, British Columbia, Canada, to northern Baja California, Mexico (Figure 1). These gastropods comprise eight genera and eight species; seven of the species are new. Nearly all of the species are very rare. The significance of this study is that the species represent either the earliest record of their genus or the first record of their genus in the Western Hemisphere. In addition to the description of the new species, their biostratigraphy is established. During the course of this study, it was discovered also that *Trochacanthus wallalense* (White, 1885), is the senior synonym of *Trochacanthus pacificus* Squires and Saul, 2001. The first photographs of White's holotype are provided here, as well as the morphologic redescription and geologic age refinement of his species.

The designated areas (e.g., Area 3) where the species were collected are shown on Figure 1. The details of the type localities are given in Appendix 1. As discussed by Saul and Squires (2008) and Squires and Saul (2009), localities west of the San Andreas Fault have been tectonically transported, and localities in British Columbia most likely have been tectonically transported from northern California. The temporal ranges of all the studied species are plotted on Figure 2. Their combined Cretaceous record in the study area spans the middle Albian to late Maastrichtian, an interval of approximately 38 million years. The paleoclimate that prevailed in the study area when the new species lived was generally warm temperate (Saul and Squires, 2008; Squires and Saul, 2009).

MATERIALS AND METHODS

This study is based on 65 specimens borrowed from museum collections. Preservation of the shell material is generally good, but nearly all the nacre has been replaced by calcite. Knowledge about the umbilical area is critical in distinguishing turbiniform-vetigastropod taxa. Some of the specimens already were already cleaned by L. R. Saul and the late W. P. Popenoe. A few additional specimens were cleaned by the author and L. R. Saul. The cleaning was done mainly by means of a

[1] Research Associate

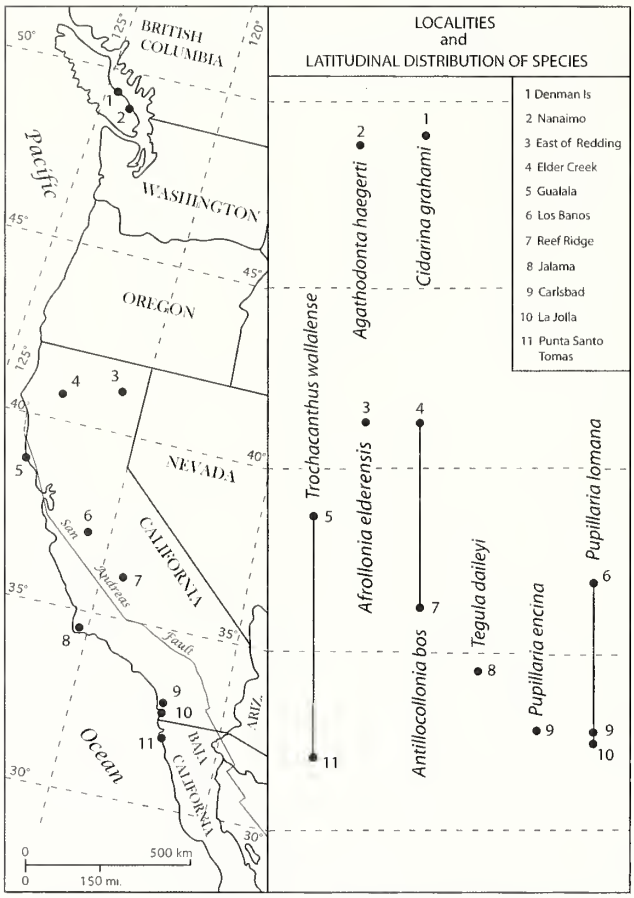


Figure 1. Localities map and latitudinal distribution of the studied trochiform vetigastropods.

high-speed drill with diamond-coated grinding wheels, but, it was also necessary to use hand-held, very sharp needles to clean the umbilical area on some of the smaller specimens.

The sequence of the treatment of the studied taxa in the "Systematic Paleontology" section mainly follows the classification scheme of Warén and Bouchet in Bouchet and Rocroi (2005: 243–245), modified to include the results from Williams et al. (2008). Most of the morphologic terms follow the usage of Cox (1960). The term "periumbilical cord" (i.e., a spiral cord extending from the parietal region downward to the columellar lip) follows the usage of Monari et al. (1996).

Current summaries of the geological details of the formations and members containing the studied specimens can be found in the following papers (listed in ascending chronostratigraphic order): Venado Sandstone (Squires and Saul, 2004a); Redding Formation, Bellavista Sandstone and Frazier Siltstone members (Squires and Saul, 2003a); Panoche Formation in Arroyo Pinoso, Reef Ridge area (Stewart, 1946); upper Haslam Formation (Squires and Saul, 2001); upper Cedar District Formation, west side of Denman Island (Squires and Saul, 2006); Jalama Formation (Squires and Saul, 2003b); Rosario Formation (Squires and Saul, 2001);

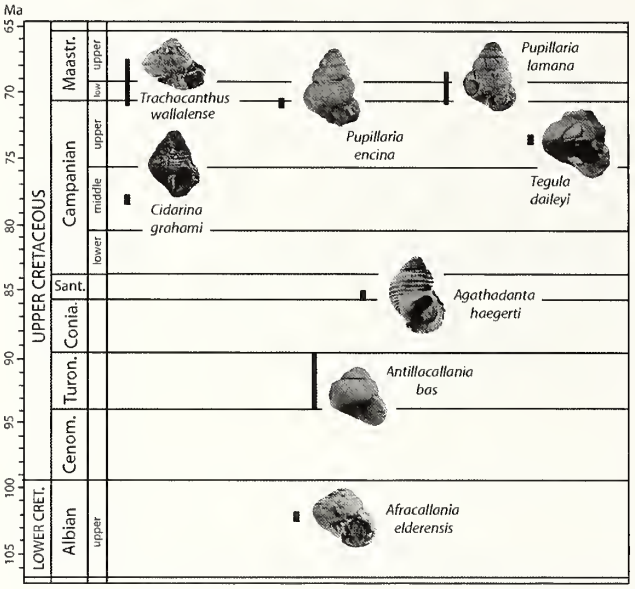


Figure 2. Geologic ranges of the studied species. Ages of stage boundaries from Gradstein et al. (2004).

Point Loma Formation (Squires and Saul, 2001); Cabrillo Formation (Squires and Saul, 2009); Gualala Formation (Squires and Saul, 2004b); and Moreno Formation, "Garzas Sand" and "Quinto Silt" members (Squires and Saul, 2003b).

Abbreviations used for catalog and locality numbers are: LACM, Natural History Museum of Los Angeles County, Invertebrate Paleontology Section (LACMIP); RBCM, Royal British Columbia Museum, Victoria; SDSNH, San Diego Society of Natural History; UCMP, University of California Museum of Paleontology (Berkeley); and USNM, National Museum of Natural History, Smithsonian Institution.

SYSTEMATIC PALEONTOLOGY

Clade Vetigastropoda Salvini-Plawen, 1980
Superfamily Amberleyoidea Wenz, 1938
Family Nododelphinulidae Cox, 1960

Genus *Trochacanthus* Dacqué, 1936

Type Species: *Trochus turberculatocintus* Münster in Goldfuss, 1844, by subsequent designation (Wenz, 1938); Late Cretaceous, Europe (Poland and Germany).

Description: Shell size small to medium. Turbinate. Phaneromphalous. Spire whorls with strong collabral ribs. Last whorl (on adults) deviantly coiled relative to spire whorls. Last whorl with single keel coincident with periphery. Umbilicus bearing thin radiating ribs separated by sunken areas.

Discussion: Except for *Trochacanthus wallalense* (White, 1885), discussed below, the only other occurrences

Figures 3–6. *Trochacanthus wallalense* (White, 1885), holotype USNM 13412, from near Gualala, California, height 16.7 mm, diameter 21.5 mm. 3. Apertural view. 4. Abapertural view. 5. Umbilical view. 6. Apical view.

of this genus are from Santonian to Maastrichtian rocks of western Germany and lower Campanian to upper Maastriehtian rocks of central Poland (Dacqué, 1936; Kollmann, 1985; Abel-Gawad, 1986).

***Trochacanthus wallalense* (White, 1885)**
(Figures 3–6)

Solarium wallalense White, 1885: 14, pl. 5, figs. 1, 2.
Trochacanthus pacificus Squires and Saul, 2001: 49, 51, fig. 3.6–3.11.

Holotype: USNM 13412, height 16.7 mm, diameter 21.5 mm.

Type Locality: Near the town of Gualala [= Wallala of White (1885)], Mendoeino County, northern California.

Geologic Age: Late Campanian to early late Maastrichtian.

Distribution: Gualala Formation, Mendoeino County, northern California (Area 5); Moreno Formation, informal Quinto member, Los Banos area, Stanislaus Coutny, northern California (Area 6); Point Loma Formation, Carlsbad, San Diego County, southern California (Area 9); Rosario Formation, Punta Santo Tomas [= Puerto Santo Tomas], Baja California, Mexico (Area 11).

Discussion: The holotype of this speeies, which is a weathered speeimen whose sculpture on the spire is not well preserved, is photographed here for the first time, with more views than White (1885) provided in his sketches. Prior to this present report, this species was known only from its type locality in the Gualala Formation in Mendocino County and [as *T. pacificus*] from the Point Loma Sandstone in San Diego County. Additional single specimens were detected during this present investigation in eolleetions from the Moreno Formation (UCMP loc. A-3224) in Merced County, California and from the Rosario Formation (UCMP loc. A-6274) at Punta Santo Tomas, Baja California, Mexico.

Superfamily Seguenzioidea Verrill, 1884
Family Chilodontidae Wenz, 1938
Subfamily Chilodontinae Wenz, 1938

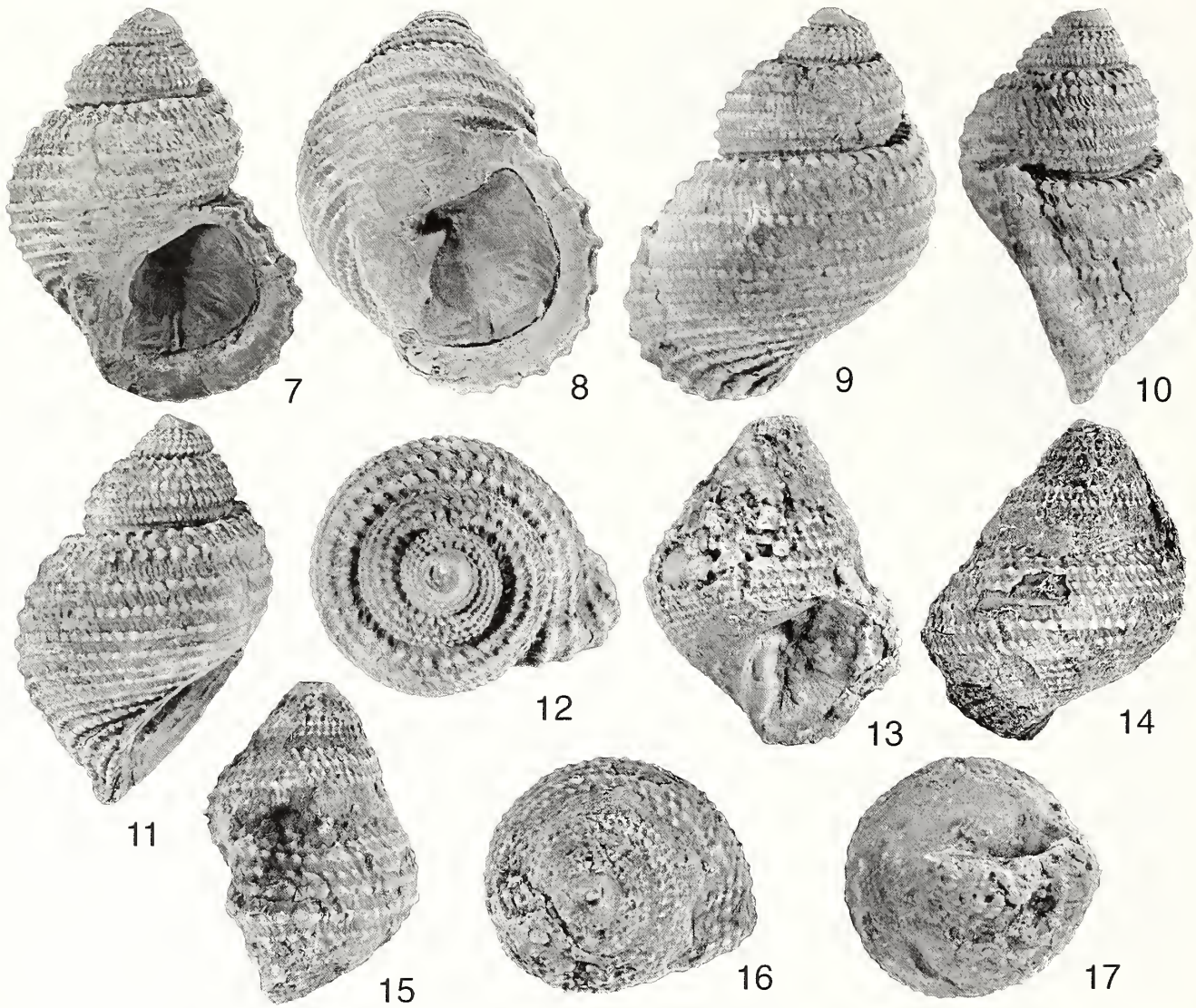
Genus ***Agathodonta* Cossmann, 1918**

Type Species: *Agathodonta elegans* (Deshayes in Leymerie, 1842 [= *Trochus dentigerus* d'Orbigny, 1842: 185, pl. 177, figs. 9–12]), by subsequent designation (Kollmann, 2005: 70–71); Early Cretaceous (Hauterivian), Franee.

Description: Shell size small to medium (height 10 to 34 mm). High fusiform. Suture deeply indented. Whorls deviantly coiled. Spiral cords strong and beaded to granulose. Outer lip variced and strongly prosoeline; interior of lip thiekened by apertural ridge with lira. Parietal eallus well developed. Columella with two widely separated teeth, posterior tooth strongest and located posteriorly up into aperture. Pustules can be present anterior to anterior tooth on columella shield (at anterior end of columella). Opereulum chitinous. Interior nacreous.

Discussion: Prior to work by Kollmann (2005: 70–71), earlier workers cited the type species of *Agathodonta* as being *Trochus dentigerus* d'Orbigny, 1842, from France. Cossmann (1918: 200–201, pl. 7, figs. 8–11) discussed and figured this species, which he identified as *Chilodonta* (*Agathodonta*) *dentigera*. Wenz (1938: 298, fig. 653) illustrated the holotype, which he identified as *Agnathodonta* [sic] *dentigera*. Cox (1960: 249, fig. 160, 2) also figured the holotype, and like Wenz, considered *Agathodonta* to be a distinct genus within the chilodontines. Cossmann (1918) and Wenz (1938) reported the range of *Agathodonta* to be Neocomian to Albian, but McLean (1984) established that this chilodontine genus ranges into the Recent, where it is represented by a single species (see also Hickman and McLean, 1990: fig. 40E) from archibenthal (300 m) depths in the Philippines.

Based on its overall shape and seulpture, the new genus is very similar to the chilodontine *Danilia* Brusina, 1865, whose type species is the extant *Monodonta tinci* Caleara, 1839, from the Mediterranean Sea. Wenz (1938: 273, fig. 572) illustrated the holotype. Beu and Climo (1974) reported that *Danilia* ranges from Albian to Recent, with the fossil species mainly of Cenomanian age in Europe. They reviewed the taxonomy of *Danilia*, compared its fossil and Recent species, and illustrated two modern speeies of this genus from New Zealand. *Agathodonta* differs from *Danilia* by having two eolumellar teeth instead of just one, teeth not showing a notched appearance, and (on some species) no pustules on eolumellar shield. *Agathodonta* superficially resembles the calliotropine *Cidarina* Dall, 1909 in terms of shape and sculpture, but the latter is smaller and does not have any columellar teeth or a flared outer lip.



Figures 7–17. New chlodontine and new calliotropine. Specimens coated with ammonium chloride. **7–12.** *Agathodonta haegerti* new species, holotype RBCM.EH2008.011.06500, Nanaimo area, British Columbia, height 33 mm, diameter 23 mm. **7.** Apertural view. **8.** Oblique apertural view. **9.** Abapertural view. **10.** Right-lateral view. **11.** Left-lateral view. **12.** Apical view. **13–17.** *Cidarina grahami* new species, holotype RBCM.EH2010.004.00001, west shore of Denman Island, British Columbia, height 18 mm, diameter 13.5 mm. **13.** Apertural view. **14.** Abapertural view. **15.** Right-lateral view. **16.** Apical view. **17.** Anterior (ventral) view.

Based on reports by earlier workers (Cossmann, 1918: 200; Wenz, 1938: 298; Keen, 1960: 1249; McLean, 1984; and Kollmann, 2005: 70–71), the geologic range of *Agathodonta* is Early Cretaceous (Hauterivian to Albian) to Recent, with its fossil occurrences restricted to Europe. *Agathodonta haegerti* new species, discussed below, is of latest Santonian age in British Columbia and is the first confirmed species of this genus in the Western Hemisphere.

***Agathodonta haegerti* new species**
(Figures 7–12)

Description: Shell size medium small (height 34 m, diameter 22 mm, same specimen). Height approximately 1.5 times greater than shell diameter. Ovate conical. Anomphalous. Spire elevated, height approximately 20% (estimated) of shell height. Pleural angle approximately 75°. Protoconch and uppermost spire unknown. Teleoconch at least four whorls. Suture deeply impressed, almost canieulate. Coiling deviant. Whorls inflated, rounded. Shoulder very narrow. Sculpture of strong widely spaced spiral ribs: four ribs on antepenultimate whorl, six on penultimate whorl, and 14 on last whorl. Interspaces between spiral ribs usually uniformly twice as wide as ribs, except near shoulder where interspaces are three times as wide as ribs. Spiral ribs on antepenultimate whorl uniformly beaded; posteriormost two spiral ribs noded on penultimate and last whorl,

other spiral ribs beaded. Aperture large, elliptical. Outer lip with varix; interior of outer lip flared and smoothish. Inner lip with two widely separated teeth, posterior tooth strongest and loeated posteriorly up into aperture. Columellar shield present in parietal arca and smooth, widening posteriorward. Growth lines prosocline. Interior naereous.

Holotype: RBCM.EH2008.011.06500, height 33 mm, diameter 23 mm.

Type Locality: Loeality 1 (see Appendix 1).

Geologic Age: Latest Santonian.

Distribution: Haslam Formation, upper part, just west of Nanaimo, east coast of Vancouver Island, British Columbia (Area 2).

Etymology: The species is named for Joe Haegert who eolleeted the holotype.

Discussion: The new speeies is based on a single speeimen. It is well preserved and is most similar to the extant *Agathodonta nortoni* McLean (1984: 122–123, figs. 1–3; Hiekman and McLean, 1990: fig. 40, E) from the Philippines. The new speeies differs by having much larger size, deviantly coiled whorls, stronger spiral ribs on shoulder of last whorl, more widely spaeed spiral ribs, absenee of having its nodes aligned in distinct collabral rows, outer lip lirae weaker and corresponding to spiral ribs rather than to their interspaces, eolumellar teeth much farther apart, anterior tooth weaker, and absence of pustules on the eolumellar shield.

The new speeies is similar to the extant *Danilia insperata* Beu and Climo (1974: 316, figs. 10–13) from New Zealand. The new speeies differs by two columellar teeth rather than one, parietal callus, no denticles on the outer lip, and no pustules on the columellar shield. The new species has the same shape as *Agathodonta? brooksi* Allison (1955: 411, pl. 40, fig. 6) from upper Aptian strata in Baja California, Mexieo. Allison was hesitant about the generie assignment of this species because of the presence of a narrow umbilicus. The new speeies differs from Allison's species by having mueh coarser sculpture that weakens rather than strengthens toward the anterior, two rather than a single columellar fold, and no umbilieus. Future collecting might show that Allison's species belongs in genus *Danilia*.

Subfamily Calliotropinae Hiekman and McLean, 1990

Discussion: Kiel and Bandel (2001: 140) stated that they did not find Hickman and McLean's definition of Calliotropinae to be "useful." Instead, they plaeed *Cidarina* Dall, 1909 in Chilodontinae Wenz, 1938 because *Cidarina* has a thick shell, whereas Calliotropinae is eharacterized by thin shells.

Genus ***Cidarina* Dall, 1909**

Type Species: *Margarita cidaris* A. Adams in Carpenter, 1864, by original designation; Pleistocene to Recent, living in Alaska to northern Baja California, Mexico (Squires and Saul, 2003b).

Description: Shell size small to medium, thin. Ovate conical. Anomphalous. Spire elevated. Sculpture of eoarse nodes or beads formed at intersections of spiral and collabral sculpture, sculpture weakest anterior to last whorl periphery, aperture nearly cireular and oblique. Umbilicus covered by thin columellar callus. Interior nacreous (Squires and Saul, 2003b).

Discussion: In their list of ealliotropines having a fossil record, Hickman and McLean (1990: 79–80) did not include the extant genus *Cidarina*. Squires and Goedert (1995) and Squires and Saul (2003) subsequently established that *Cidarina* does have a fossil reeord. *Cidarina grahami* new species is the earliest *Cidarina*. Only four fossil species of *Cidarina* were previously known: *Cidarina cretacea* Squires and Saul (2003b) of upper Campanian to mid Maastriehtian age from the southern half of California; *Cidarina beta* Squires and Saul (2003b), of mid-Maastrichtian age from central California; *Cidarina antiqua* Squires and Goedert (1995) of middle Eocene age ("Tejon Stage") from southwestern Washington; and *Cidarina cidaris* (A. Adams in Carpenter, 1864) of early Pleistocene to Recent age on the Paeifie slope of North America from Alaska to northern Baja California (Grant and Gale, 1931).

***Cidarina grahami* new species**
(Figures 13–17)

Diagnosis: *Cidarina* with medium shell size, spiral ribs nodose posterior to periphery, spiral ribs on base elosely spaeed, base of last whorl bearing weak spiral ribs with numerous, closely spaced minute nodes.

Description: Shell size medium (height 18 mm, diameter 13 mm, same speeimen). Height approximately 1.4 times shell diameter. Ovate conieal. Spire elevated, approximately 35% of shell height. Pleural angle 64°. Protoconeh and upper spire unknown. Teleoeoneh ineomplete, at least three whorls. Suture apparently impressed. Spire whorls flat-sided, body whorl convex, rounded but with peripheral angulation. Shell surfaee covered by spiral ribs: four on ante-penultimate whorl, five on pentultimate whorl, six on posterior half (including peripheral angulation) of last whorl, and ten on base of body whorl. Spiral ribs bearing fine beads on upper spire whorls and on base of last whorl; spiral ribs bearing medium-strength beads on penultimate whorl; spiral ribs bearing strong nodes on posterior half of last whorl and on first rib anterior to periphery, with strongest nodes on peripheral angulation. Aperture moderately elliptieal. Outer lip thin. Inner lip and columella with grooved eallus elosing off umbilicus. Callus wash extends over parietal area. Growth lines prosocline, tilted 16° from vertieal.

Holotype: RBCM.EH2010.004.00001, height 18 mm, diameter 13.5 mm.

Type Locality: Locality 2 (see Appendix 1).

Geologic Age: Late middle to early late Campanian (*Metaplacenticeras* cf. *pacificum* ammonite zone).

Distribution: Cedar District Formation, upper part, west side of Denman Island off east coast of Vancouver Island, British Columbia (Area 1).

Etymology: The species is named for Raymond Graham, who informed the author about the existence of this species.

Discussion: The new species is based on a single specimen, which has good preservation. The new species is most similar to *Cidarina cretacea* Squires and Saul (2003b: 52, fig. 2.1–2.4) from Maastrichtrian strata of central California and (new information) from the upper Campanian to possibly lower Maastrichtian Point Loma Formation at the Carlsbad Research Center, San Diego County, southern California. The new species differs from *C. cretacea* by having more closely spaced spiral ribs with slightly coarser ornament posterior to the periphery on the last whorl, and fewer spiral ribs but with coarser ornament on the base of the last whorl.

Superfamily Turbinoidea Rafinesque, 1815
Family Turbinidae Rafinesque, 1815
Subfamily Colloniinae Cossmann in Cossmann and Peyrot, 1916

Discussion: McLean and Kiel (2007) provided a review of the systematic treatment of turbinoids and colloniines, including some reservations about recent molecular data (e.g., Williams and Ozawa, 2006) concerning these groups. Stemming from Cossmann's early work, it has been recognized (e.g., Hickman and McLean, 1990; McLean and Kiel, 2007) that opercular information is important in dealing with colloniines. Monari et al. (1996) pointed out, however, that in fossil material, information about the operculum is unavailable except in extremely exceptional cases, hence, it is nearly impossible to base a useable paleontological classification on opercula. They argued that other morphological shell characters can be used to distinguish members of colloniines, which constitute a rather homogeneous group in having a thick shell that is smooth or weakly ornamented with spiral threads.

Genus ***Afrollonia*** **Adegoke, 1977**

Type Species: *Afrollonia nigerensis* Adegoke, 1977, by original designation; Paleocene, southwestern Nigeria.

Description: Shell size small. Turbiniform. Phaneromphalous. Spire low to moderately high. Ramp broad. Protoconch small, smooth, and bulbous. Teleoconch sculpture consisting of few fine spiral ribs. Anterior end of columellar lip slightly expanded and subangulate where intersected by carination of umbilical margin; umbilical rim usually prominent and crenulated, interior of umbilicus with periumbilical cord ending in a wide process on columella (Adegoke, 1977; Kase, 1984).

Discussion: *Afrollonia* is similar to genus *Collonia* J. E. Gray in M. E. Gray, 1850, but differs from the latter by having sculpture. Although Adegoke (1977) assigned *Afrollonia* to subfamily Colloniinae, Kase (1984) assigned this genus to subfamily Margaritinae Stoliczka, 1868 based on the similarity of *Afrollonia* to *Atira* Stewart, 1927, which was originally proposed as a subgenus of *Margarites* J. E. Gray, 1847 (*ex* Leach ms.). This similarity is superficial because *Afrollonia* is characterized by a periumbilical cord; no such feature is present on *Atira*.

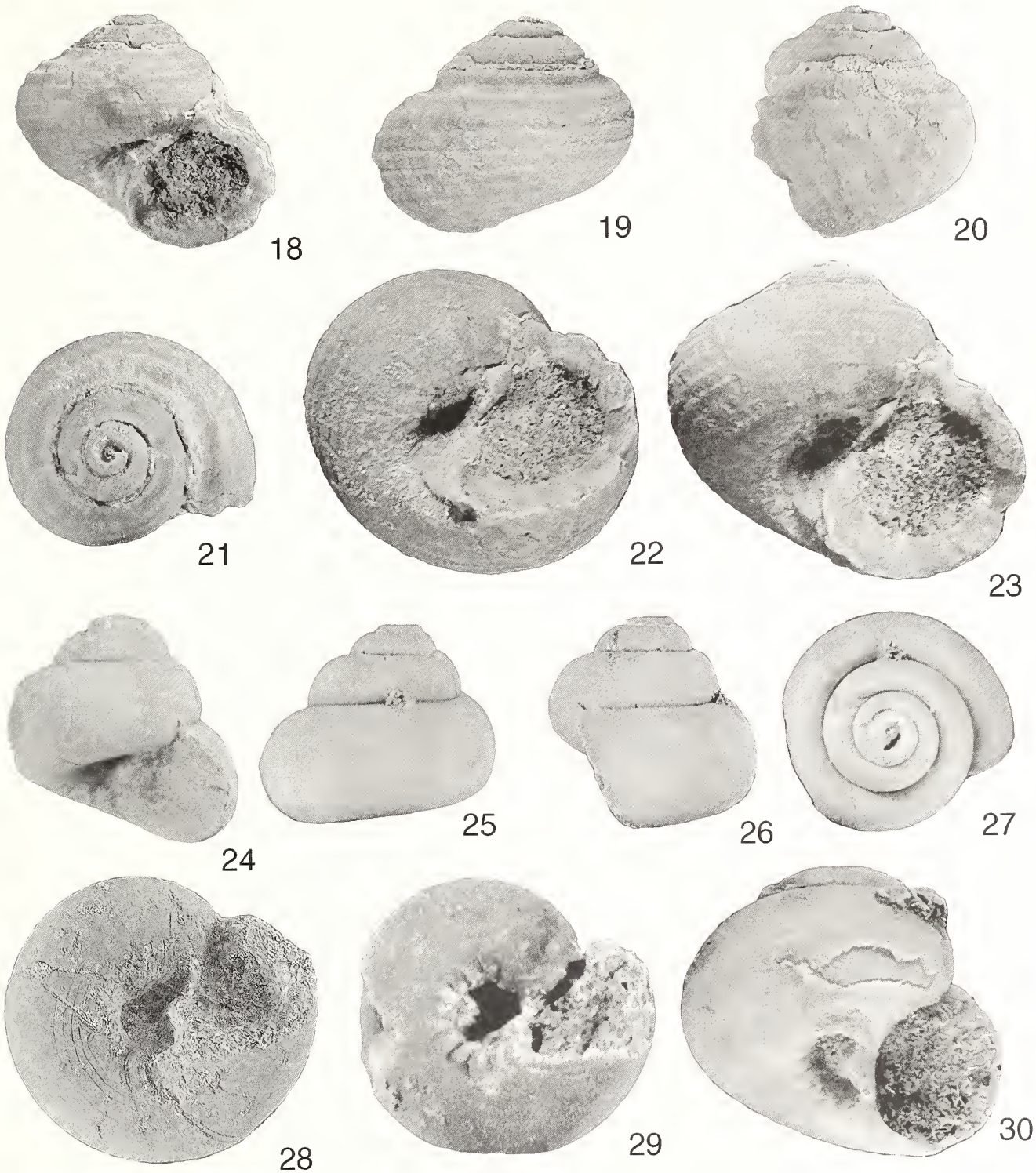
Afrollonia has been reported only from Paleocene strata in Egypt, Nigeria, and Togo, Africa (Adegoke 1977). *Afrollonia elderensis* new species, described below, is the earliest confirmed record of this genus and its only record in the Western Hemisphere.

Afrollonia elderensis **new species**
(Figures 18–23)

Diagnosis: *Afrollonia* with rounded whorls, suture collared, spiral ribs moderately widely spaced, umbilicus rim weakly demarcated.

Description: Shell size small (up to height 6 mm, diameter 6.5 mm, same specimen). Height slightly less than shell diameter. Turbiniform. Phaneromphalous. Spire moderately low, height approximately 28% of shell height. Pleural angle approximately 105°. Protoconch unknown. Teleoconch consisting of approximately four whorls. Suture impressed and rimed by thin, high collar on succeeding whorl. Whorls rounded. Ramp on last whorl concave. Sculpture on spire whorls consisting of approximately three to four, narrow but widely spaced spiral threads with smooth, concave interspaces. Sculpture on last whorl consisting of several thin, prominent, and widely spaced spiral ribs; approximately five spiral ribs between suture and base on last whorl. Interspace between collar and posteriormost spiral rib widest and most concave. Base not clearly demarcated from sides of last whorl. Sculpture on base consisting of seven spiral ribs, most being weaker than those on periphery but becoming anteriorly stronger. Aperture circular. Outer and inner lips flared. Peristome continuous. Umbilicus semi-lunar. Rim of umbilicus subtle and demarcated near inner lip by short but strong and noded spiral rib increasing in strength toward anterior end of aperture. Periumbilical cord smooth, extending short distance into umbilicus on its left side. Columellar lip reflected toward umbilicus adjacent to terminus of periumbilical cord. Anterior end of columellar lip slightly expanded and subangulate where intersected by carination of umbilical margin. Growth lines prosocline.

Holotype: LACMIP 13701, height 6 mm, diameter 6.7 mm.



Figures 18–30. New collonnines. Specimens coated with ammonium chloride. **18–23.** *Afrollonia eldercnsis* new species, holotype LACMIP 13701, LACMIP loc. 28777, height 6 mm, diameter 6.7 mm. **18.** Apertural view. **19.** Abapertural view. **20.** Right-lateral view. **21.** Apical view. **22.** Umbilical view. **23.** Oblique umbilical view. **24–30.** *Antillocollonia bos* new species **24, 25, 26, 27.** Holotype LACMIP 13702, LACMIP loc. 10742, height 6.5 mm, diameter 6.5 mm. **24.** Apertural view. **25.** Abapertural view. **26.** Right-lateral view. **27.** Apical view. **28.** Paratype LACMIP 13703, Stewart's (1946) Arroyo Pinoso, loc. 97, umbilical view, diameter 7 mm. **29.** Paratype LACMIP 13704, LACMIP loc. 10763, umbilical view, diameter 5 mm. **30.** Paratype LACMIP 13705, LACMIP loc. 10742, oblique umbilical view, diameter 5.8 mm.

Type Locality: LACMIP 28777.

Geologic Age: Late Albian.

Distribution: Reworked Albian material in the Turonian Venado Sandstone, Elder Creek, Tehama County, northern California (Area 4).

Etymology: Named for its occurrence in Elder Creek area, Tehama County, northern California.

Discussion: The new species is based on a single specimen, which has good preservation. The exact location of the type locality of the new species is not known. It is a boulder from a conglomerate of early Turonian age, but, according to the LACMIP locality information, the fauna in the boulder is of late Albian age. Reworked late Albian fossils in this same stratigraphic unit are known elsewhere in the Cretaceous section of northern Sacramento Valley, northern California (Matsumoto, 1960: 34–35; Popenoe et al., 1960: chart 10e; Squires and Saul, 2006).

The new species is most similar to *Afrollonia nigeriensis* Adegoke (1977: 68–69, pl. 11, figs. 10–15) from Paleocene rocks in southwest Nigeria but differs from Adegokes' species by having a flatter ramp, last whorl not ornamented by three prominent spiral ribs with much finer spirals in between, base not angulate, and umbilical rim not well demarcated.

Kase (1984) reported *Afrollonia matsushimensis* Kase (1984: 60–61, pl. 6, figs. 5, 8–10) from upper Aptian to lower Albian strata in northeastern Japan. Kase's species, however, does not have a periumbilical ridge nor a thickening of the columella where this ridge intersects the columella; hence, his species does not belong in this genus.

Genus ***Antillocollonia* Sohl, 1998**

Type Species: *Antillocollonia brujoensis* Sohl, 1998, by original designation; late Campanian to Maastrichtian, Puerto Rico.

Description: Small size small (less than 10 mm high) but sturdy. Turbinate. Phaneromphalous. Teleoconch whorls smooth. Aperture circular. Peristome continuous. Periumbilical cord prominent and smooth. Columellar lip thickest where intersected by periumbilical cord. Anterior end of columellar lip slightly expanded and subangulate where intersected by carination of umbilical margin. Exterior of operculum pustulose, ridge, and with prominent central pit (Sohl, 1998). Rim of umbilicus with or without crenulations.

Discussion: *Antillocollonia* is similar to *Collonia* M. E. Gray, 1850 but differs from the latter by having an auricular (earlike) projection high on the columella and lacking beads on the umbilical rim.

Antillocollina has been reported before only from upper Campanian to Maastrichtian strata in Puerto Rico (Sohl, 1998). *Antillocollina bos* new species, described below, is the earliest record of this genus and is also its first record from the Pacific slope of North America.

***Antillocollonia bos* new species**
(Figures 24–30)

Diagnosis: *Antillocollonia* with umbilicus rim usually coincident with coarsely noded spiral cord, anteriormost two nodes strongest.

Description: Shell size very small (up to height 6.5 mm, diameter 7 mm, same specimen). Height approximately same as shell diameter. Turbinate. Phaneromphalous. Spire moderately high, height approximately 20% of shell height. Pleural angle 89°. Protoconch unknown. Teleoconch consisting of six whorls. Suture impressed. Whorls convex. Shoulder very narrow. Shell surface smooth; base of last whorl can have five to six, very faint, flat, and widely spaced spiral bands with incised striae between them. Aperture circular. Outer lip thin, inner lip thicker. Peristome continuous. Umbilicus narrow. Rim of umbilicus angulate and usually demarcated by coarsely noded spiral rib, nodes commonly increasing in strength toward anterior end of aperture; anteriormost node strongest; nodes on posterior part of rim generally less well developed on adult specimens; spiral rib terminates at columellar lip. Periumbilical cord prominent, smooth. Columellar lip thickest where intersected by periumbilical cord. Anterior end of columellar lip slightly expanded and subangulate where intersected by carination of umbilical margin. Growth lines prosocline.

Holotype: LACMIP 13702, height 6.5 mm, diameter 6.5 mm.

Paratypes: LACMIP 13703–13705.

Type Locality: LACMIP 10742.

Geologic Age: Turonian.

Distribution: LOWER TURONIAN: Redding Formation, Bellavista Sandstone Member, east of Redding, Shasta County, northern California (Area 3). MIDDLE TURONIAN: Redding Formation, Frazier Siltstone Member, east of Redding, Shasta County, northern California (Area 3). TURONIAN (UNDIFFERENTIATED): Panoche Formation, Arroyo Pinoso, Reef Ridge area, Fresno County, central California (Area 7).

Etymology: Named for its occurrence in Cow Creek area east of Redding, Shasta County, northern California; *bos*, Latin, meaning cow.

Discussion: The examined material consisted of 52 specimens. Preservation is good although the fragile periumbilical cord is usually missing or incomplete. Some specimens do not have nodes on the rim of the umbilicus.

The new species is remarkably similar to *Antillocollonia brujoensis* Sohl (1998: 47–48, pl. 3, figs. 17–22)

from upper Campanian to Maastrichtian strata in Puerto Rico. The main difference is that the new species commonly has a coarsely noded spiral rib on the rim of the umbilicus.

The new species superficially resembles the trochid *Garramites nitidus* Stephenson (1941: 262, pl. 47, figs. 17–19) from the Nacatoch Sand, eastern Texas. Stephenson (1941) assigned this sand to the Maastrichtian, but Akers and Akers (1997: fig. 2) assigned it to the upper Campanian. Genus *Garramites* Stephenson, 1941, which is monotypic, is characterized by a nearly smooth small shell having a wide umbilicus with an angulated, rather coarsely crenulated rim. Within the umbilicus is a broad, shallow, spiral sulcus that closely rims the row of prominent crenulations. *Anticollonia bos* differs from *G. nitidus* by having a periumbilical cord and commonly having a beaded ridge that rims the umbilicus. In addition, *A. bos* does not possess a spiral sulcus that closely rims this beaded ridge.

The occurrence of the new species in the Panoche Formation in Arroyo Pinoso of the Reef Ridge area, Fersno County, central California is based on the author's observation of specimens from Stewart's (1946: 88) locality 97. Stewart noted that W. P. Popenoe identified the fauna from this locality as Turonian in age, and Popenoe et al. (1960: 1521) reiterated this interpretation.

Family Turbinidae? Rafinesque, 1815
Subfamily Tegulinae Kuroda, Habe, and Oyama, 1971

Discussion: This subfamily was previously generally believed to be a trochid subfamily (e.g., Hickman and McLean, 1990), but, based on molecular studies of extant taxa by Williams et al. (2008), it has been provisionally assigned to the Turbinidae.

Genus ***Tegula*** **Lesson, 1835** ***sensu lato***

Type Species: *Tegula pellisserpertis* (Wood, 1828), by original designation; Recent, west coast of Central America to Gorgona Island, Colombia, South America (Keen, 1971).

Description: Shell size medium, solid. Globose to conic. Phaneromphalous. Shells smooth to sculptured, with sculpture consisting of broad, coarsely beaded spiral ribs. Base flattened. Peristome discontinuous. Anterior end of columella with one or more teeth. Umbilicus ranging from open to closed. Interior nacreous.

Discussion: Based on reports by earlier workers (Wenz, 1938; Keen, 1960), the geologic range of *Tegula* is Miocene to Recent. Subsequently, other workers (Bandel and Stinnesbeck, 2000; Kiel and Bandel, 2001; Squires and Saul, 2005) demonstrated that *Tegula* has a Cretaceous record, and the earliest known species is *Tegula jeanae* Squires and Saul, 2005 of early Campanian age in northern California.

Tegula daileyi **new species**
(Figures 31–33)

Diagnosis: *Tegula* with three to four widely spaced, narrow spiral ribs on penultimate and last whorls.

Description: Shell size medium (height 19 mm, diameter 19 mm, same specimen). Height approximately same as shell diameter. Turbinate. Phaneromphalous. Spire unknown. Suture impressed. Penultimate and last whorls convex with three to four narrow, prominent spiral ribs; widely and subequally spaced, with two anteriormost ribs slightly closer to each other. Base flattened, apparently smooth. Aperture circular. Peristome interrupted. Outer lip moderately thin. Inner lip with single prominent tooth. Umbilicus small. Growth lines prosocline, tilted 43° from vertical.

Holotype: LACMIP 13706, height 20.4 mm, diameter 20.7 mm.

Type Locality: LACMIP 24123.

Geologic Age: Late Campanian.

Distribution: Jalama Formation, Santa Barbara County, California (Area 8).

Etymology: The species is named for D.H. Dailey who worked on the molluscan fauna from the Jalama Formation.

Discussion: The new species is based on a single specimen, which is crushed and missing its spire. It is most similar to the extant *Tegula mariana* (Dall, 1919: 359; Keen, 1971: fig. 105), known mainly from the Gulf of California, Mexico, but differs from Dall's species by having a larger size, higher spire, and a more prominent columellar tooth.

The new species differs from *Tegula jeanae* Squires and Saul (2005: 135–136, figs. 3–5), of early Campanian age from northern California, by having sculpture, an open umbilicus, more prominent columella tooth, no secondary denticles in the columella, and no raised lip along the basal edge of the interior of the last whorl. Bandel and Stinnesbeck (2000) reported *Tegula ovallei* (Philippi, 1887) from Maastrichtian strata in central Chile. The new species differs by not having numerous, closely spaced and beaded spiral ribs. Kiel and Bandel (2001) reported *Tegula? simplex* (Quintero and Revilla, 1966) from the Campanian (undifferentiated) strata of northern Spain. The new species differs by having a much larger shell, an umbilicus, and an absence of numerous, closely spaced spiral ribs.

Subfamily Margaritinae Stoliczka, 1868

Discussion: This subfamily was previously generally believed to be a trochid subfamily (e.g., Hickman and McLean, 1990; Warén and Bouchet in Bouchet and Rocroi, 2005), but, based on molecular studies of extant taxa by Williams et al. (2008), it has been provisionally assigned to the Turbinidae. According to Willams et al. (2009), Margaritinae is not monophyletic.

Figures 31–44. New tegulne and new margaritnes. Specimens coated with ammonium chloride. **31–33.** Tegulne *Tegula daileyi* new species, holotype LACMIP 13706, LACMIP loc. 24123, height 20.4 mm, diameter 20.7 mm. **31.** Apertural view. **32.** Right-lateral view. **33.** Umbilical view. **34–37.** *Pupillaria encina* new species, holotype SDSNH 11082, SDSNH loc. 152, height 11.7 mm, diameter 8.6 mm. **34.** Apertural view. **35.** Abapertural view. **36.** Apical view. **37.** Umbilical view. **38–44.** *Pupillaria lomana* new species, holotype LACMIP 13707, LACMIP loc. 5571, height 12.2 mm, diameter 9.6 mm. **38.** Apertural view. **39.** Abapertural view. **40.** Right-lateral view. **41.** Apical view. **42.** Umbilical view. **43–44.** Paratype LACMIP 13708, LACMIP loc. 5571, juvenile, height 6.8 mm, diameter 7 mm. **43.** Abapertural view. **44.** Left-lateral view.

Genus ***Pupillaria*** **Dall, 1909**

Type Species: *Trochus pupillus* Gould, 1849, by original designation; Recent, Bering Sea to southern California.

Description: Shell size small to moderately small, thin. Turbiniform to ovate-conical. Phaneromphalous. Spiral ribs raised but flattened with narrow interspaces. Peristome discontinuous. Columella smooth. Outer lip unthickened. Umbilicus slit-like to nearly closed. Interior nacreous.

Discussion: Workers (e.g., Wenz, 1938; Palmer, 1958; Keen, 1960) traditionally used *Pupillaria* as a subgenus of *Margarites*. The narrowness of the umbilicus of *Pupillaria*, however, warrants that *Pupillaria* have generic standing. According to Wenz (1938) and Keen (1960), the geologic range of *Pupillaria* is Miocene to Recent. The new species *Pupillaria encina* and *Pupillaria lomana*, described below, extend the earliest record of *Pupillaria* to the late Campanian.

Pupillaria encina **new species**
(Figures 34–37)

Calliomphalus? sp. Sundberg and Riney, 1984: table 1.

Diagnosis: *Pupillaria* with ovate-conic shape and broad and prominent spiral ribs.

Description: Shell size small (up to height 11.7 mm, diameter 8.6 mm, same specimen). Height approximately 1.3 times shell diameter. Ovate conical. Phaneromphalous. Spire high, approximately two-thirds of shell height. Pleural angle 52°. Protoconch unknown.

Teleoeonch approximately six whorls. Suture impressed. Shoulder rounded. Sculpture consisting of many broad spiral ribs; five on upper spire whorls, seven on penultimate whorl, approximately 13 on last whorl and becoming narrower anteriorward of periphery. Interspaces very narrow and incised. Aperture eireular. Peristome discontinuous? Umbilieus slit-like and extremely narrow. Growth lines prosoeline, tilted 20° from vertical.

Holotype: SDSNH 11082, height 11.7 mm, diameter 8.6 mm.

Type Locality: SDSNH 152.

Geologic Age: Late Campanian to possibly early Maastrichtian.

Distribution: Point Loma Formation, Cañon de Las Encinas, near Carlsbad, San Diego area, San Diego County, southern California (Area 9).

Etymology: The new speeies is named (noun in apposition) for its occurrenee at Cañon de Las Encinas; Spanish, *encina*, meaning "oak."

Discussion: The new species is based on a single speeimen, whieh is the non-figured specimen of *Calliomphalus*? sp. reported by Sundberg and Riney (1984) from the Carlsbad Research Center, San Diego County. This species differs from *Pupillaria lomana* new species by having wider and more prominent spiral ribs and no interrib between the spiral ribs on the posterior part of the last whorl.

***Pupillaria lomana* new species**
(Figures 38–44)

Diagnosis: *Pupillaria* with spiral ribs narrow and single fine interrib between spiral ribs on posterior part of last whorl.

Description: Shell size small (up to height 12 mm, diameter 9.5 mm, same specimen). Height approximately 1.3 times shell diameter. Ovate eonieal. Phaneromphalous. Spire high, approximately two-thirds of shell height. Pleural angle 54°. Protoconch unknown. Teleoconch approximately six whorls. Suture impressed. Shoulder rounded. Sculpture consisting of numerous elosely spaeed, narrow spiral ribs; six to seven on spire whorls, 16 to 18 on last whorl and becoming narrower anteriorly of periphery. Spiral ribs just posterior of suture strongest and minutely beaded. Spiral ribs on shoulder weak, approximately two and widely spaced. Interspaces between spiral ribs on posterior of last whorl with single spiral riblet. Aperture eireular. Outer lip thin; inner lip very slightly thickened anteriorly. Peristome discontinuous? Umbilieus slit-like, nearly closed. Growth lines prosoeline, tilted 25° from vertical.

Holotype: LACMIP 13707, height 12.2 mm, diameter 9.6 mm.

Paratype: LACMIP 13708.

Type Locality: LACMIP 5571.

Geologic Age: Late Campanian to possibly early Maastrichtian.

Distribution: Moreno Formation, "Quinto Silt" member or possibly "Garzas Sand" member, Los Banos Creek, Merced County, northern California (Area 6); Point Loma Formation at the Carlsbad Research Center, Carlsbad, San Diego County, southern California (Area 9); Cabrillo Formation (in a reworked clast from the underlying Point Loma Formation), La Jolla, San Diego County, southern California (Area 10).

Etymology: The new species is named for the Point Loma Formation.

Discussion: The examined material consisted of four specimens. Preservation is good. The new species is like the speeimen of the extant *Pupillaria pupilla* (Gould, 1849) illustrated by Hiekman and McLean (1990, fig. 48, two figs.), but differs from their specimen by having much more impressed sutures.

The new species resembles *Margarites kasei* Kiel and Bandel (2001:31, pl. 5, figs. 16–17) from the Campanian (undifferentiated) of northern Spain, but the new speeies differs by having a wider pleural angle, wider spire whorls, and mueh stronger spiral sculpture.

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Raymond Graham and Joe Haegert (Victoria Palaeontology Society, Victoria, British Columbia) kindly provided excellent specimens with good locality data from the Nanaimo Group, Vancouver Island area. LouElla R. Saul (LACMIP) expertly cleaned the aperture of the holotype of *Agathodonta luegerti*. James H. McLean (LACM, Malaeology) shared his vast knowledge of vetigastropod genera. The following people facilitated the loan of speeimens: Paul Callomon (ANSP), Harry Filkorn (LACMIP), Lindsey T. Groves (LACM, Malacology), Jann Thompson (Smithsonian Institution), Mark Goodwin (UCMP), and Scott Rugh, Pat Don Vito, and Kesler Krandall (SDSNH). Lindsey T. Groves (LACM, Malaeology) also provided some important references.

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APPENDIX 1 – TYPE LOCALITIES OF THE NEW SPECIES

Listed quadrangle maps are U. S. Geological Survey maps. Detailed information about the other cited localities is available via the following: LACMIP website: <http://ip.nhm.org/ipdatabase/locality_show>; UCMP website: <http://ucmpdb.Berkeley.edu/loc.html>; and CAS: contact the collections manager.

Locality 1. "Lower Quarry," just west of Nanaimo, 49°11.735′ N, 124°6.143′ W, at the Moto-cross racetrack on Dumont Road, east coast of Vancouver Island, British Columbia. Haslam Formation, upper part. Age: Latest Santonian. Collector: Joe Haegert, 1987.

Locality 2. Gray siltstone, slightly north of "White House Site," near ferry terminal, west shore of Denman Island, 49°32′16.2″ N, 124°49′37.7″ W, off east coast of Vancouver Island, British Columbia. Cedar District Formation, upper part. Age: Late middle Campanian to early late Campanian (*Metaplacenticeras* cf. *pacificum* Zone). Collector: R. Graham, March 28, 2005.

LACMIP 5571. Elevation 10 ft., gray argillaceous and coarse sandstone concretion (Point Loma Formation lithology) on beach, approximately 20 m N of concrete/gully at W most end of Forward St., La Jolla, La Jolla Quadrangle (1953, 7.5 minute), San Diego, southern California. Clast of Point Loma Formation reworked into the Cabrillo Formation. Age: Late Campanian or possibly early Maastrichtian. Collector: B. Welton, August 16, 1977.

LACMIP 10742. Fine-grained sandstones and sandy shales on S bank of Little Cow Creek at the approximate

S line of the SE 1/4 of the SW 1/4 of section 36, T. 33 N, R. 3 W, Millville Quadrangle (15 minute, 1953), Shasta County, California. Redding Formation, Frazier Siltstone Member. Age: Middle to late Turonian. Collectors: W. P. Popenoe and G. P. Zebal, August 1, 1941.

LACMIP 10798. Lat. 40°38′00″ N, long. 122°04′30″ W. Massive sandstones interbedded with conglomerates on S side of high E–W trending ridge, 998 m (3275 ft.) S54°59′W from SE corner of section 10, T. 32 N, R. 2 W, Millville Quadrangle (15 minute, 1953), south side of Oak Run Valley, Shasta County, northern California. Redding Formation, Member V. Age: Early Santonian. Collectors: W. P. Popenoe and C. W. Ahlroth, July 1, 1936.

LACMIP 24123. Hard, medium to coarse-grained, gray pebbly arkosic sandstone, near of ridge, 525 ft. north of Jalama Creek, elevation 625 ft., 2.42 mi. E and 0.68 mi. S of the Jalama Ranch Headquarters, 2.29 mi. W and 0.42 mi N of the SE corner of the topographic sheet, Lompoc Hills Quadrangle (1947), Santa Barbara County, California. Jalama Formation. Age: Late Campanian. Collector: D. Dailey, August, 1958.

LACMIP 28777. From boulder in basal "Chico" conglomerate, Elder Creek, Tehama County, northern California. Collector: P. R. Reinhart.

SDSNH 152. Cañon de Las Encinas, Rancho Agua Hedionda, San Diego County, California. Point Loma Formation. Age: Late Campanian or possibly early Maastrichtian. Collector: F. Stephens, March 29, 1929.

Giant fossil *Acharax* (Bivalvia: Solemyidae) from the Miocene of Japan

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ABSTRACT

Specimens of *Acharax yokosukensis* recently collected from the upper lower Miocene Kokozura Formation of the Takaku Group in Ibaraki Prefecture, central Japan, served as the basis for a re-description of the species. These specimens include a valve of the largest specimen of this genus known worldwide, exceeding 295.7 mm in length. The occurrences of the giant *Acharax* species in Japan are confined to lower to lower middle Miocene sediments deposited in tropical shallow and deep environments.

Additional keywords: Chemosynthesis, bivalves, deep-sea

INTRODUCTION

Solemyidae is the oldest group of chemosymbiotic bivalves, ranging back to the Ordovician (Taylor and Glover, 2010; Kiel, 2010). Among them, the oldest confirmed member of the extant genus *Acharax* is known from the early Cretaceous in Hokkaido, northern Japan (Kiel et al., 2008), but there are many unidentified solemyids from the older geological record that may also belong to *Acharax*. Two species of *Acharax* are known to live in Japanese waters: *A. johnsoni* (Dall, 1891) and *A. japonicus* (Dunker, 1882). The latter species is small and lives in shallow water (0–20 m depth; Habe, 1977) and has been found in settling tanks of sea water at a marine laboratory (Yamanaka et al., 2008). In contrast, *A. johnsoni* has a large shell attaining 150 mm in length (Kamenev, 2009), similar to other deep-water *Acharax* species, and lives in deep water (the depth range of *A. johnsoni* is very wide; according to Kamenev (2009) the species may be found from 100–5379 m. However, 100 m seems to be an exceptional case. Kamenev's data and JAMSTEC data show this species usually lives in deeper than 370 m.) The largest living species of *Acharax* is *A. bartschii* described by Dall (1908b) from the Philippines, with a shell length of 191 mm.

Notwithstanding problems with their identification, fossil *Acharax* in Japan are more diverse than extant species. Eleven species have been recorded from deposits of Cretaceous to Pliocene age (Kanie and Kuramoehi, 2002; Kiel et al., 2008). The largest known species is *A. gigas* from the Miocene Haratajino Formation with a length reaching 264.1 mm (Kanie et al., 1999; Kurihara, 2000). Taylor and Glover (2010) cited a specimen of *A. yokosukensis* Kanie and Kuramochi, 1995, from the Miocene Hayama Group in Kanagawa Prefecture, central Honshu, as the largest *Acharax* in the world, referring to "a fossil *Acharax* from the Miocene [that] measured a massive 300 mm". However, Kanie and Kuramoehi (1995) only estimated that, based on a fragment of a shell.

We collected an imperfect specimen of *A. yokosukensis* having a length of 295.7 mm from the Miocene Kokozura Formation of the Takaku Group exposed along Pacific coast in Kitaibaraki City, in the northern part of Ibaraki Prefecture, central Honshu. So far, this specimen is the largest *Acharax* recorded worldwide. In this paper, we describe *A. yokosukensis* and speculate about why it could have evolved to such large size.

MATERIALS AND METHODS

The specimens described herein were collected from boulders present in the uppermost lower Miocene Kokozura Formation that may constitute the base layer under the Izura Kanko Hotel (Figure 1). These boulders with a diameter of around 1 m consist of sandy limestone or calcareous fine-grained sandstone including many shells and trace fossils (Figure 2). Ueda et al. (2005) differentiated these calcareous concretions into six morphological types. Among them, type I concretions (large irregularly shaped carbonates) show negative $\delta^{13}C$ value ranging from –29.4 to –20.9‰. These values indicate that the carbonates precipitated under the influence of the oxidation of hydrocarbons such as crude oil or methane with an influx of marine bicarbonate (Kiel and Peckmann 2007). The boulders yielding the large *Acharax yokosukensis* specimens resemble type I concretions in size and shape.

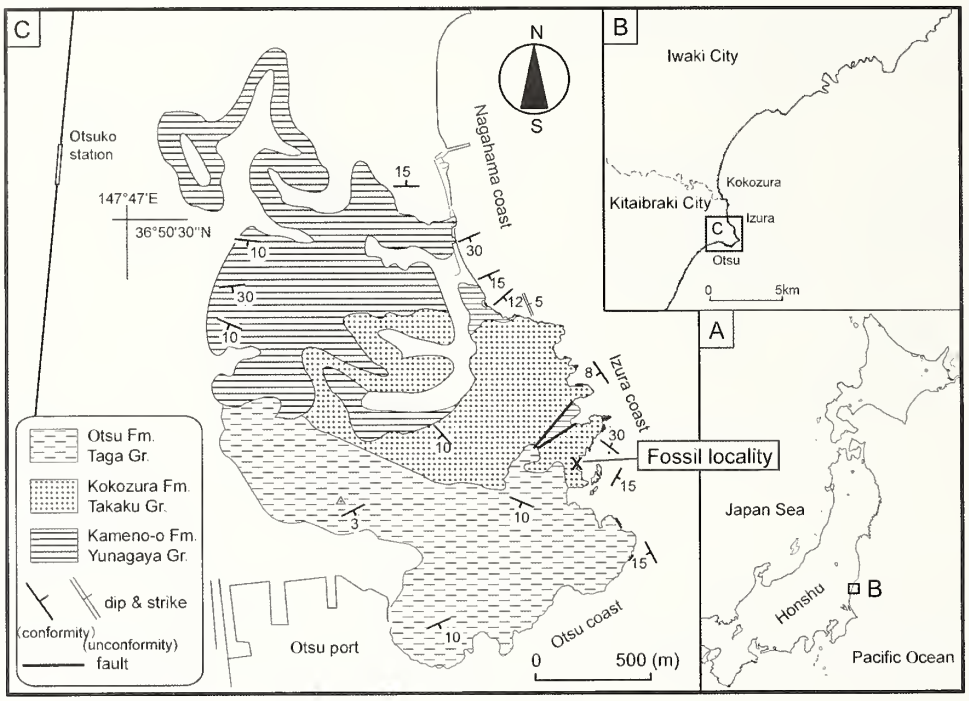


Figure 1. Locality map. Geological map adapted from Ueda et al. (2005).

Figure 2. Occurrence of *Acharax yokosukensis* in a calcareous concretion block.

The age of the Kokozura Formation of the Takaku Group in this area was assigned to the uppermost lower Miocene *Crucidenticula kanayae* zone (NPD 3A zone; NPD = Neogene North Pacific Diatom) by Yanagisawa (1996), based on diatom fossils. From the sedimentary facies and the occurrence of heterotrophic bivalves like *Mizuhopecten kobiyamai* (Kamada) and *Cylocardia siogamensis* (Nomura), these sediments were considered to be deposited on the muddy sand shelf (Ueda et al., 2005).

The fauna associated with *Acharax yokosukensis* is a blend of chemosymbiotic bivalves and predatory gastropods. The chemosymbiotic species include the lucinids *Lucinoma acutilineatum* (Conrad) and *Nipponothracia*? sp., the thyasirid *Conchocele bisecta* (Conrad), and the vesicomyids *Callogonia*? sp. and *Adulomya* sp. The predatory gastropod species are represented by a few specimens of the naticid *Cryptonatica clausa* (Broderip and Sowerby) and the turrid *Megasurcula yokoyamai* (Otuka).

For comparing the shell proportion of *Acharax yokosukensis*, some Recent specimens of *A. johnsoni* from northern Pacific, stored at National Science Museum in Tokyo were examined.

Abbreviations used in text: JUE=Joetsu University of Education; YCM-Gp = Yokosuka City Museum.

SYSTEMATICS

Family Solemyidae

Genus ***Acharax* Dall, 1908**

Type Species: *Solemya johnsoni* Dall, 1891

***Acharax yokosukensis* Kanie and Kuramochi, 1995**
(Figures 3–10)

Acharax aff. *tokunagai* (Yokoyama).—Ogasawara et al., 1994: 34–35, figs. 3-1a-c.
Acharax n. sp. —Kanie et al., 1995: 57–58, figs. 1, 2-1-3, 3-2-4.
Acharax yokosukensis Kanie and Kuramochi, 1995: 52, 56, figs. 1–4; Kanie and Kuramochi, 2002: 56, figs. 2–13.

Holotype: YCM-Gp Ig36.

Material Examined: Eight specimens including one almost perfect specimen. JUE nos. 15887-1~8.

Figures 3–10. *Acharax yokosukensis* (Kanie and Kuramochi). **3–5, 7–10.** Specimens from the Kokozura Formation. **3–5.** JUE no. 15887-2, right valve. **3.** Rubber east of hinge of the specimen illustrated in Figure 5, hinge length, 82.9 mm. **4.** Rubber cast of outer shell surface of the specimen illustrated in Figure 5, length 168.4 mm. **5.** Inner mold, length 155.1 mm. **7.** Rubber cast of outer shell surface, JUE no. 15887-3, length 195.2+ mm, right valve. Most posterior part and some ventral part are missing. **8.** Rubber east of inner shell surface, JUE no. 15887-4, length 109.9 mm, left valve. **9, 10.** JUE no. 15887-1, left valve. **9.** Inner mold, length 244.7 mm. **10.** Rubber cast of outer shell surface, length 295.7+ mm. **6.** Holotype from the Hayama Group. YCM-Gp Ig36, length 144.1 mm, right valve.

Description: Shell exceptionally large for genus, exceeding 295.7 mm in length (Table 1), elongate quadrate, height/length-ratio = 0.40–0.44, equivalve and inequilateral, moderately inflated. Umbo situated nearly central or slightly posteriorly (anterior length: AL/ shell length-ratio = 0.52–0.61). Anterior margin subtruncate; ventral margin nearly straight; antero-dorsal margin nearly straight; postero-dorsal margin very broadly

Table 1. Measurements (mm) of valves of *Acharax yokosukensis*.

Specimens	Length	Height	H/L	AL	AL/L	Valve
JUE no. 15887-1						left
(rubber east of outer surfaee)	295.7+	108.5	–	–	–	
(inner mold)	244.7	107.3	0.44	127.6	0.52	
JUE no. 15887-2						right
(rubber east of outer surface)	168.4	66.7	0.40	102.2	0.61	
(inner mold)	155.1	60.9	0.39	92.7	0.60	
JUE no. 15887-3						
(rubber east of outer surfaee)	195.2+	–	–	–	–	right

arehed, continuing into well-rounded posterior margin. Hinge edentulous and inner surface of subumbonal part radially grooved. Nymph opisthodetie. Anterior adduetor muscle scar indistinct; posterior adductor muscle scar large, quadrate, deeply impressed and crenulated by distinct radial grooves. Surface sculptured by fourteen radial ribs; five distinct, low and wide radial ribs in anterior part; five fine and round-topped radial ribs with very wide interspaces in middle part; four round-topped radial ribs with narrower interspaees in posterior part.

Remarks: As pointed by Kanie and Kuramochi (1995), *Acharax* aff. *tokunagai* (Yokoyama) described by Ogasawara et al. (1994), from the lower Miocene Aokiyama Formation in Chiba Prefecture, is a synonym of *A. yokosukensis*. These authors reaehed this conelusion because of the species centrally situated beak and similar number of ribs (11 in the Aokiyama specimens).

Comparison: *Acharax gigas* (Kanno, 1960) from the Miocene Hiranita and Haratajino formations resemble *A. yokosukensis* in its huge shell size (264.1 mm in length). However, *A. gigas* can be distinguished from *A. yokosukensis* in having a smaller height/length-ratio (more elongate shell, H/L = 0.25–0.34), and a more posteriorly situated beak (AL= 0.65–0.78) (Figures 11, 12). The Recent species, *Acharax johnsoni* (Dall, 1891) differs from *A. yokosukensis* by its smaller shell and more posteriorly situated beak (AL = 0.70–0.77) (Figures 11, 12).

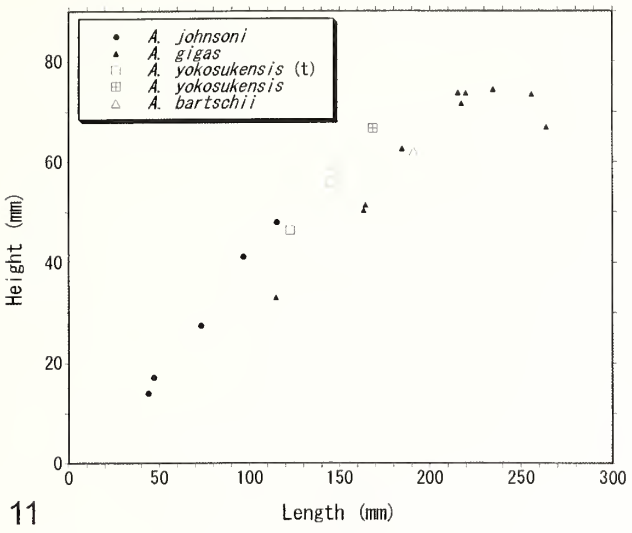
Distribution: Lower Miocene Aokiyama Formation in Chiba Prefecture; upper lower Miocene Kokozura Formation of Takaku Group in Ibaraki Prefecture; lower middle Miocene Hayama Group in Kanagawa Prefecture.

DISCUSSION

The giant specimens of *Acharax yokosukensis* reported here were recovered from probable hydrocarbon seep deposits in the lower to lower middle Miocene sediments in the northeastern Kanto District, central Honshu (Figure 13). Another giant *Acharax* species, *A. gigas* has also been recorded from ancient seep sites in the Hiranita and Haratajino Formations in the northwestern Kanto District, correlated with zone N8 of Blow (1969) (latest early to earliest middle Mioeene), based on the examination of planktonic foraminiferans (Takahashi, 1992; Oishi and Takahashi, 1990). This Miocene age corresponds to the mid-Neogene Climatic Optimum (Tsuchi, 1987). At that time, a tropical elimate prevailed in what is now the Kanto District (Ogasawara, 1994). Other than the occurrence of the Kokozura specimens, these giant *Acharax* were from deep seep sites. Exceptionally, the largest specimen of *A. yokosukensis* was recovered from the shallow seep deposits of the Kokozura Formation. Thus, regardless of depth, the warm climate and methane seep environment might affect the size of fossil *Acharax*.

Like solemyids, lueinid bivalves are ehemosymbiotic, deep burrowers, and geologically old members of the seep fauna, whieh first appeared in the Jurassic (Kiel, 2010). Oecurrences of large fossil lucinids were summarized by Taylor and Glover (2009) who described the largest lucinid, *Superlucina megameris* (Dall) that reached 280 mm in length and 311 mm in height. According to their list, the large lueinids appeared in geological ages with warm elimates like the late Jurassic-early Cretaceous, middle Eoeene, and middle Miocene. In deposits younger than the early Pliocene, the occurrences are mostly confined to tropical areas like the Philippines and Taiwan. Moreover, large lucinids were recovered from both shallow and deep sites like the giant *Acharax*.

Generally speaking, the maximum size of largest species of each guild in the eoastal marine tropics correlates or correlated with the marine productivity (Vermeij, 2011). Solemyids are well known to have a reduced gut or to lack an alimentary tract, and to depend on their chemoautotrophic symbionts for nutrition (Stewart and Cavanaugh, 2006; Taylor et al., 2008). It seems thus plausible that chemosynthetic species need to take up a lot of sulfide to achieve a large size (Taylor and Glover, 2009). Assuming that warm temperatures facilitate physiological process like sulfide uptake, the warm temperatures of the latest early to earliest middle Miocene might have played a role in the gigantism of the *Acharax* specimens reported here, although the exact mechanisms are unknown. At modern seeps, *Acharax* often lives at the periphery away from the highest sulfide concentrations (Sahling et al., 2002). Thus, for obtaining sulfides, the lack of competition might also play a role.



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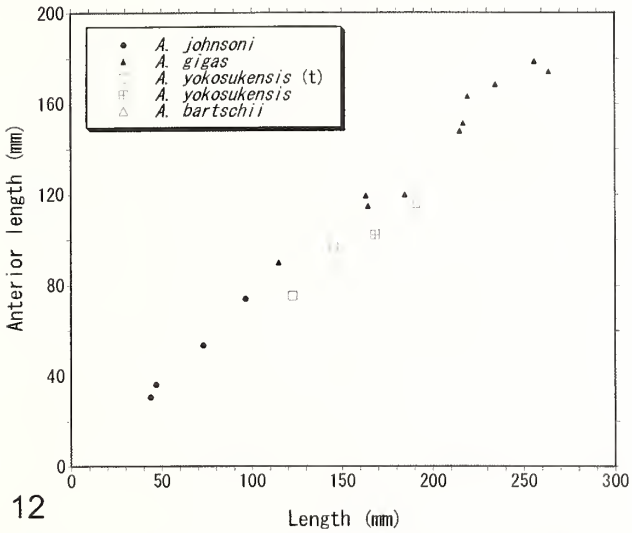

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Figures 11–12. Ontogenetic changes in *Acharax yokosukensis* (t: type material), *A. johnsoni*, *A. gigas*, and *A. bartschii*. The largest shell of *A. yokosukensis* is incomplete and excluded from both graphs. Dimensions of *A. yokosukensis* and the recent specimens of *A. johnsoni* were measured by hand. Data for *A. gigas* and *A. bartschii* respectively from Kanie et al. (1999) and Dall (1908b). **11.** Shell length and height. **12.** Shell length and anterior length.

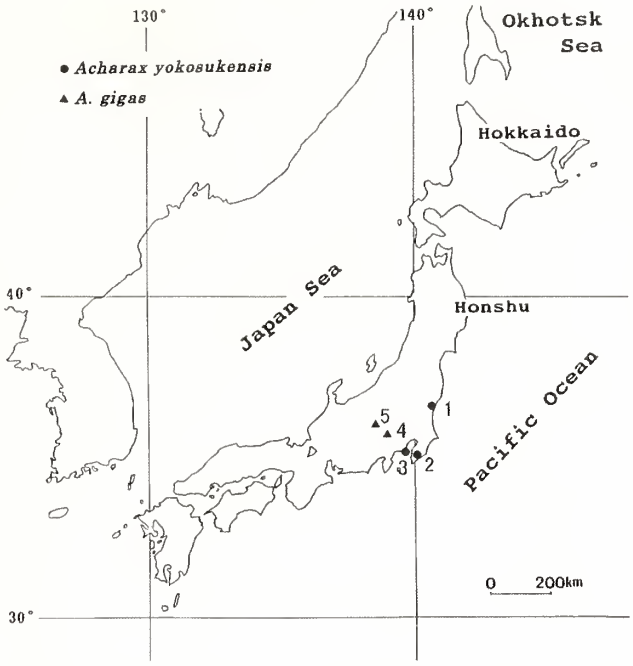

Figure 13. Distribution of *Acharax yokosukensis* and *A. gigas*. 1. Kokozura F.; 2. Aokiyama F.; 3. Hayama G.; 4. Hiranita F.; and 5. Haratajino F.

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Redescription of the genus *Modiomytilus* Griffin, 1990 (Bivalvia: Mytilidae) from Southern Patagonia with remarks on the paleobiogeography of the genus

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ABSTRACT

Modiomytilus Griffin, 1990, was based on composite molds collected from Cenozoic rocks in southern Patagonia. The type speeies eomes from the early Miocene Centinela Formation, exposed along the southern shore of Lake Argentino. An additional species is known from the Eocene Río Turbio Formation, which outcrops only at the southwestern corner of Santa Cruz Province. New material preserved as original shell was eollected recently in beds referred to the Centinela Formation exposed in the same area as the Río Turbio Formation, about 150 km south of Lake Argentino. Enough detail is preserved in eolleeted the shells to warrant an emended diagnosis and a new and more complete description of the genus, as they provide a set of characters not recorded in the currently known material of any of the speeies deseribed. The shells elearly belong to the type species, i.e., *Modiomytilus argentinensis* Griffin, 1990. These characters, among which are included the ligament, adductor muscle scar, pallial line, and byssal retractor muscle sear allow a reinterpretation of this genus and eonfirm its validity. At the same time these new morphological characters may be potentially useful for further phylogenetic analyses and a new interpretation of the currently available material, a prerequisite for understanding the palaeobiogeographie history of this genus.

Additional keywords: Early Miocene, middle Eocene, shell morphology

INTRODUCTION

The genus *Modiomytilus* was introduced to include two species, *Modiomytilus argentinesis* Griffin (1990: 377–380), from the early Miocene Centinela Formation, and *Modiomytilus mercerati* Griffin (1990: 380–381, fig. 1, 2) from the Eocene Río Turbio Formation, in Santa Cruz Province. The genus description was based on composite molds in which no part of the shell was preserved. Also belonging in this genus are *Mytilus* aff. *chorus hauthali* Molina sensu Ihering (1907: 273–274), from the "Patagonian" beds in the Ñirihuau basin (northern Patagonia) and *Mytilus pseudochorus* Doello-Jurado (1922: 86–90, fig. 1) from the "Patagonian" beds of Sierra de los Baguales (Santa Cruz), and additional non-figured specimens from San Julián. *Mytilosootus arcuatus* Stilwell and Zinsmeister, (1992: 54–56, pl. 3 fig. a), from the Eocene La Meseta Formation in Seymour Island, Antarctica, was based on an internal mold belonging in *Modiomytilus* too.

The aim of this contribution is to re-describe this genus more accurately based on new specimens recently collected in the Centinela Formation in southwestern Santa Cruz. This material confirms some of the original diagnostic characters and reveals the presence of other particular features that better distinguish this taxon from other Mytilidae. Among these are shell thickness, the presence of a well developed and buttressed anterior adductor muscle scar coalescent with a large byssal retractor scar, and a pitted resilial ridge, together with a thickened hinge plate with growth lines only. Biogeographic and stratigraphic distributions of the species involved suggest that the genus had an austral origin and a lifespan ranging from the at least the late Eocene through the early Miocene. Its ecological requirements probably played an important role, as it is not common. However, in the beds where it does occur—deposited in shallow, possibly restricted marine environments—it is usually abundant, and sometimes the only mollusk taxon present.

The specimens studied are deposited at the División de Paleozoología de Invertebrados Collection, Museo de La Plata, Buenos Aires, Argentina (MLP). The term ichnospecies is abbreviated "isp."

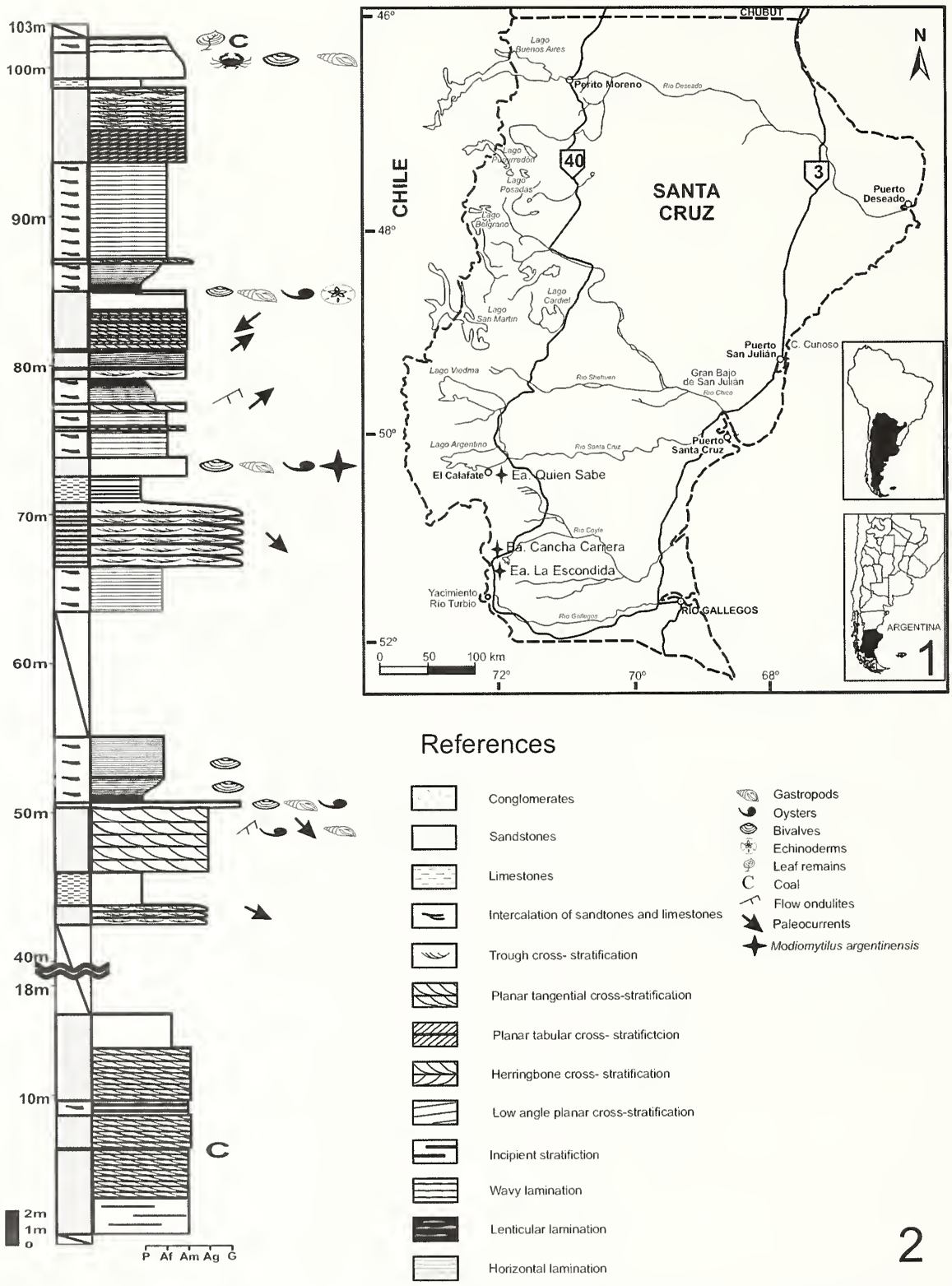


Figure 1–2. Location map and stratigraphic section. 1. Location map of the fossil locality in Santa Cruz Province, Argentina. 2. Studied stratigraphic section showing bed with mytilids.

GEOLOGICAL SETTING
(Figure 2)

Rocks deposited during the Cenozoic Patagonian transgression are included in several units of slightly variable lithology and exposed over a wide area of Patagonia. Located in the southwestern corner of Santa Cruz Province, these rocks are known as Centinela Formation (Furque and Camacho, 1972). This unit is discontinuously exposed along the foothills of the Andes for a distance of about 500 km, approximately between Lake Pueyrredón (47°48′ S, 70°47′ W) and Estancia La Escondida (51°24′ S, 72°10′ W). The new specimens collected come from this southernmost locality, where the Centinela Formation overlies the continental plant and coal-bearing Oligocene Río Leona Formation (Figure 1).

Marenssi et al. (2005) reported that the Río Leona Formation comprises a fining-upward succession of facies deposited in high-energy fluvial environments at the base, giving way to low energy maeandriform and anastomosed rivers at the top. Such a variation in the fluvial style of this unit is probably linked to the palcogeographic evolution of the southwestern corner of the Austral Basin. The base probably represents a high gradient piedmont context, while the top of the unit reveals the presence of a low coastal plain at the time the unit was deposited. Approximately 25 to 22 million years ago this coastal plain was covered by the Patagonian transgression. Accordingly, the Río Leona and Centinela formations constitute a depositional sequence of Oligocene to early Miocene age (Marenssi et al., 2002).

At the fossil locality studied, the Centinela Formation comprises fine to medium sandstones, sometimes with fossil mollusks, with subordinate conglomeradic sandstones, fine conglomerates, coquinas and mudstones deposited in a shallow littoral marine environment (Malumián et al., 2000). Contact with the overlying Santa Cruz Formation is masked by Recent deposits. However, the restricted outcrops of the Centinela Formation in the area and the fact that the Santa Cruz Formation in some places directly overlies the Río Leona Formation suggest that there may be an unconformity separating the two units (Malumián et al., 2000).

The studied locality lies within land belonging to Estancia La Escondida, about 20 km to the north of the mining town of Río Turbio. Contrary to localities in the Lake Argentino area, at Estancia La Escondida the Centinela Formation is thinner and geographically restricted, i.e., it is exposed only along a narrow 12 km N–S stretch between Estancia Las Tres Marías (51°30′00″ S, 72°16′67″ W) and Estancia La Primavera (51°27′00″ S, 72°13′60″ W) (Malumián et al., 2000).

The section is 103 m thick and contact with the underlying Río Leona Formation is transitional, as at other localities in southwestern Santa Cruz such as Estancia 25 de Mayo and Estancia La Siberia (Casadío et al., 2000; Rodríguez Raising et al., 2006). Because of the loose and poorly resistant nature of the pelitic facies at the top of the Río Leona and bottom of the Centinela formations, the contact itself is not exposed.

The lowermost exposed beds of the Centinel Formation are about 16 m of medium cross-stratified sandstones with pelitic layers bounding the fore-sets. At the base of some of the sets there are thin layers of conglomerates and coarse sandstones. These beds carry *Ophiomorpha* isp. Intercalated among them are medium to fine sandstones and heterolithic beds.

The overlying 26 m are covered, probably because they include loose hetherolithic facies that are easily meteorized, as observed at other localities where the unit is exposed such as Estancia La Siberia (Rodríguez-Raising et al., 2006). The section continues upward with 24 m of mudstone and hetherolithic beds with medium- to coarse-grained sandstone and subordinate conglomerates. The coarser facies carry a rich invertebrate fauna and burrows referred to *Thalasinoides* isp. and *Ophiomorpha* isp.

Overlying these beds are 4.5 m of coarse sandstone and conglomerates with trough cross-stratification, followed by 1.5 m of siltstone and 1.25 m of fine to medium muddy sandstone with abundant remains of bivalves —including the studied mytilids. At the base of the sandstone there are bivalve burrows excavated into the underlying mudstone. This bed carries *Valdesia dalli* (Ihering, 1897); *Perissodonta ameghinoi* (Ihering, 1897); *Polinices santacruzensis* Ihering, 1907; *Modiomytilus argentinensis* Griffin, 1990 (disarticulated and bioeroded); *Gregariella* sp.; *Modiolus arctus* (Feruglio, 1935); *"Ostrea" hatcheri* Ihering, 1902 (right valve); *Cardium* sp. (disarticulated); Tellinidae indet.; *Retrotapes striatolamellata* (Ihering, 1907); *Panopea bagualesia* Ihering, 1899 (in life position); *Panopea nucleus* (Ihering, 1899); *Laternula* sp. Some of the valves are lying convex down with abundant bioerosion on their inner surface. Specimens of *Panopea* in life position are common and one articulated *Laternula* was observed.

The next 28 m are heterolithic beds with medium sandstones with cross-stratification and constituting cosets up to 5 m thick. Two sandstone beds carry bivalve shells, some of them (*Panopea* sp.) in life position, echinoderms, gastropods, and —within the bed closest to the top of the section— crab remains. The top of the section includes heterolithic beds with leaves and plant debris.

The presence of *Panopea* in life position suggests that the bed carrying most of the fossils was deposited in a subtidal environment. Bioerosion and encrusting of the shell inner surface suggest that they laid exposed on the sea floor during a period of low sea level long enough to allow colonization. The abundance of shells with different degrees of weathering also suggests a period with low sedimentation. According to these observations, the mytilid-bearing bed was deposited during a low sedimentation period in a subtidal normal marine environment. This could be linked to a maximum flooding surface of the Patagonian transgression in the area.

SYSTEMATIC PALEONTOLOGY

Superfamily Mytiloidea Rafinesque, 1815
Family Mytilidae Rafinesque, 1815
Subfamily Modiolinae Keen, 1958

Genus ***Modiomytilus* Griffin, 1990**

Type Species: *Modiomytilus argentinensis* Griffin, 1990; original designation.

Description: Shell modioliform, umbones not terminal; well defined ridge running in a wide curve from umbones to posterior ventral end; ligament about one half of total length of shell; anterior part contained within narrow, deep ligament groove running along dorsal margin of thickened hinge plate; resilial ridge not preserved, but regular pits along posterior part of nymphs suggest that it was pitted (Figure 4); pits wider dorsally, ventrally narrowing, and curving forward to join preceding ones into anterior groove; obsolete posterior lateral tooth on right valve and shallow groove on anterior hinge plate; anterior adductor muscle scar (AAMS) large, placed on low buttress, with anterior part encroached by vertical wall of thick anterior part of shell (Figure 3); vertical wall with well marked rounded pits and with short strong irregular ribs near intersection with AAMS, running perpendicular surface of latter; surface of AAMS with strong parallel ridges, reflecting on prismatic layer the underlying ribs on inner shell surface in this region; anterior retractor muscle scar large and rounded, placed at dorsal posterior end of buttress supporting AAMS (Figure 5); pallial line strongly incised, irregularly pitted, meeting AAMS (Figure 6); nacreous inner surface; ornamentation of commarginal undulations (Figure 7).

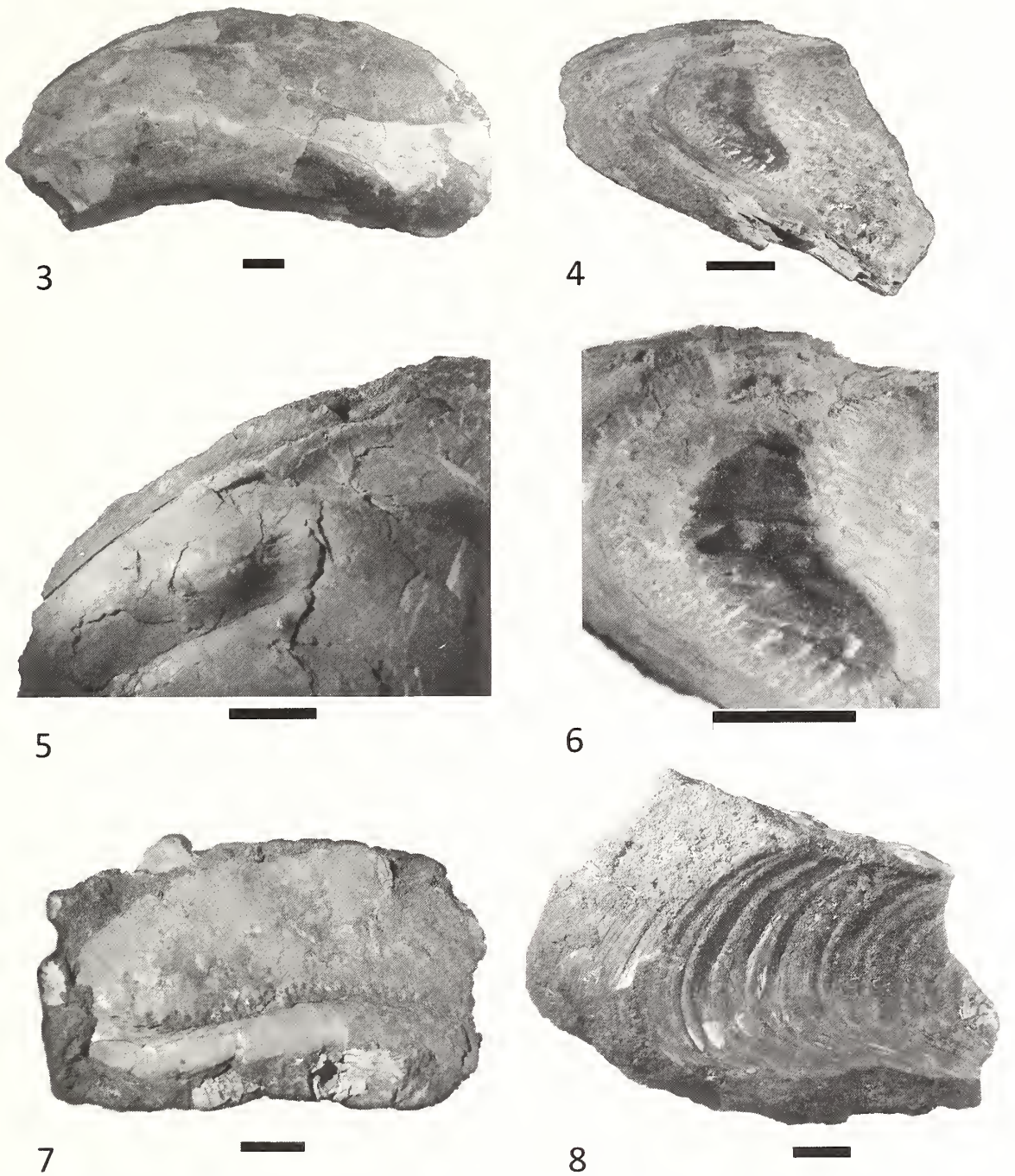
Species Included: The type species *Modiomytilus argentinensis* Griffin, 1990 comes from the early Miocene Centinela Formation exposed along the southern margin of Lake Argentino, in southwestern Santa Cruz. The additional material described herein was collected from rocks referable to this unit as exposed at Estancia La Escondida approximately 40 kilometers north of Río Turbio. The oldest species recorded are the Eocene *Modiomytilus arcuatus* (Stilwell and Zinsmeister, 1992) from the La Meseta Formation in Antarctica (Stilwell and Zinsmeister, 1992, p. 54–56, pl. 3 fig. a), and *Modiomytilus mercerati* Griffin (1990: 380–381, figs 3–4), from the Río Turbio Formation in southwestern Santa Cruz. *Modiomytilus pseudochorus* (Doello-Jurado, 1922, p. 3–6, fig. 1) is known only by the type specimens, which come from the early Miocene Monte León Formation exposed at the mouth of the Santa Cruz River. No additional material has ever been reported of this species. *Modiomytilus hautlali* (Ihering, 1907) occurs in Cenozoic beds exposed in northwestern Patagonia (Ihering, 1907), probably equivalent to the Monte León and Centinela formations.

Remarks: Species of *Modiomytilus* could not be included in any of the currently accepted supraspecific taxa of Cenozoic Mytilidae. *Mytilus* Linnaeus (1758: 104) has a proportionally much more reduced anterior adductor muscle scar and thinner shells; the external ornamentation is smooth, while in *Modiomytilus* the shell surface shows commarginal undulations. *Aulacomya* Mörch (1853: 53) differs considerably by its radial ribs, its lack of an anterior adductor muscle, and its unpitted resilial ridge. *Perna* Retzius (1788: 20) shows—as does *Modiomytilus*— a pitted resilial ridge and a nacreous inner surface, but it is missing an anterior adductor muscle scar. The Recent *Mytella* Soot-Ryen (1955: 47) shares the pitted resilial ridge but the commarginal ornamentation of this genus is much weaker and regular. The southern Pacific *Notobotula* Fleming, (1959: 170), has a quite large muscle scar very much like that of *Modiomytilus* but shows no evidence of the strong parallel ridges, and it lacks commarginal ornamentation except for growth lines. The Recent *Semimytilus* Soot-Ryen (1955: 25), from the west coast of South America, differs by its compact resilial ridge and smooth surface. The Oligocene–Recent *Crenomytilus* Soot-Ryen (1955: 23), shows a distinct thickened anterior adductor scar like in *Modiomytilus*, but without the complexity of the scar surface of the latter; it also presents terminal umbones, a compact resilial ridge, and an obliquely striated shell that is clearly different from *Crenomytilus*. *Choromytilus* Soot-Ryen (1952: 121) is easily distinguishable because of its compact resilial ridge, the absence of an anterior adductor muscle, its typical hinge tooth, and its smooth surface.

***Modiomytilus argentinensis* Griffin, 1990**
(Figures 2–7)

Modiomytilus argentinensis n. sp.; Griffin, 1990: 379–380, figs. 1, 2

Description: Shells large (maximum estimated length = 154.5 mm), mytiliform, with subterminal anterior umbones. Dorsal margin convex and smoothly merging into narrowly curved posterior margin. Ventral margin concave, maximum concavity just in front of shell midlength. Shell thickness very variable depending on area of shell. Shell very thick at umbonal end, reaching 14.47 mm at the posterior end of the AAMS). Shell thinning out in a posterodorsal direction, measuring only a few millimeters at posterodorsal end. Anterior margin strongly thickened just below umbones; margin forming a narrow marginal plate densely packed with growth lines, reflecting the shell thickness at this sector of the valves. Hinge without traces of dentition. Ligament running along approximately 0.6 mm of dorsal margin, which is slightly thickened to hold resilial ridge. Anterior part of preserved ligament groove narrow and curved along anterior dorsal margin. Ligament groove occupying a wider strip along margin towards posterior end, ending abruptly and bounded by a faint ridge weakening even further towards the dorsal margin, which it does not



Figures 3–8. *Modiomytilus argentinensis*. **3.** Specimen with conjoined valves (anterior end missing), showing remains of inner layer of shell, MLP-23197. **4.** Right valve internal view showing a general view of the anterior adductor muscle scar (AAMS) and-well developed hinge plate, MLP-23190. **5.** Detail of ligament showing marks of pitted resilial ridge along dorsal margin. Specimen decorticated, MLP-23197. **6.** Detail of the AAMS. Note subspherical protuberance on AAMS surface. Also anterior vertical surface and strong ridges beneath AAMS surface, MLP-23190. **7.** Left valve internal view showing irregulary pitted pallial line, MLP-23182. **8.** External mold of right valve showing commarginal folds (posterior half of shell), MLP-23205. Scale bars = 1 cm.

reach in any of the available specimens. Ligament groove showing clearly pitted nature of resilial ridge at mid-length, evident in specimens with shell material partly adhered to internal molds, but not so in specimens in which shell is missing, including the type specimens. Area between resilial ridge and dorsal margin of shell flat, but crossed by very shallow curved depressions that begin at resilial ridge and widen towards margin

(Figure 5). Internal surface of shell generally smooth and not reflecting external ornamentation, but showing anterior adductor muscle scars, anterior byssal retractor scars, pallial line and granulations. AAMS placed near anterior end, large (20.7 mm × 13.3 mm), buttressed andand kidney-shaped, i.e., scar evenly rounded anteriorly and showing a fairly deep concavity at mid-length posteriorly; anterodorsal half of AAMS more inflated, posterior half slightly more elongated; AAMS bounded anteriorly by steeply inclined inner surface of shell (forming an angle of about 100°), acquiring again an approximately horizontal position near margin, thus rendering a reflected appearance to anterior inner shell surface. Surface of AAMS not smooth, but covered by straight anteroposteriorly directed rods, subquadrangular in section and more densely packed and thicker against anterior boundary of scar, tapering towards posterior edge of AAMS. Vertical surface of shell immediately adjacent to anterior outline of AAMS densely reticulated. AAMS surface with a hemispherical knob-like structure at mid-width and at base of anterior half of scar. Muscle pad rapidly sloping down to general shell surface behind posterior edge of AAMS, but not as steeply as rising shell surface anterior to scar. Anterior byssal retractor muscle scar large, rounded, placed just above AAMS pad as it meets anterodorsal margin of shell. Pallial line entire, strongly marked, and pitted throughout its preserved length, especially along ventral concave margin of shell. Posterior adductor muscle scars unavailable for observation, because posterior region of shell was not preserved in examined specimens. Outer surface of shell strongly ornamented with commarginal undulations. Intercostal spaces crossed by fine and barely noticeable radial striations.

Geological Occurrence: All specimens come from the upper section of the Centinela Formation exposed at Estancia La Escondida, located about 20 km North of the mining town of Río Turbio, Santa Cruz Province (51°24′21.76″ S, 72°10′2.35″ W).

Material Examined: MLP-23180: three RV internal molds partly covered by shell matter; MLP-23182: two left valve fragments with shell, showing pitted pallial line; MLP-23186: two fragments of anterior end RV, shell preserved, showing a pitted resilial ridge and anterior adductor muscle scar; MLP-23190: three anterior end fragments of RV, internal view,shell preserved, showing anterior adductor muscle scar; MLP-23195: a fragment of internal mold of LV, shell preserved on margins. MLP-23197: one specimen with valves conjoined without the anterior end, showing remains of inner layer of shell; MLP-23199: LV internal mold fragment with preserved shell on ventral margin; MLP-23205: fragment of external mold of RV, showing commarginal folds; MLP-23212: fragment of anterior RV.

Remarks: The description provided above differs substantially from the original description of this species and consequently from the original generic description, as all previously known specimens consisted of only internal and composite molds in which many characters now available were not observed. Thus, a new interpretation of this taxon strengthens the taxonomic placement suggested for other species in which the shell still remains unknown. The muscle scar appears as a strong pad, more or less oval in outline. Width of pad is about 50% of length. However, the new specimens described herein show a number of distinct peculiarities of this muscle scar that cannot be observed in any of the molds previously available. Among these are the numerous vertical striations on the shell surface that bound the muscle scar anteriorly. These striations are a conspicuous feature of the shells, but are not preserved on the molds.

Comparison of this species with the other species referred to this genus must necessarily be tentative, until specimens of the latter are found with preserved shells. However, the original comparisons of *Modiomytilus argentinensis* with *Modiomytilus mercerati* are confirmed by the new material described herein. The type series of *M. argentinensis* are all composite molds showing no traces of shell. Nevertheless, the size and shape of the anterior adductor muscle scars agree perfectly with those in the new shells from Estancia La Escondida. The shell interior of these appears to be smooth (except for the muscle scars and granulated texture on some areas). On the composite molds, this surface is superimposed onto the outer shell ornamentation, which shows the same wavy and anastomosing pattern as the shells newly described herein.

Similarly, all known specimens of *Modiomytilus mercerati*, Griffin, 1990 are composite molds. While the ornamentation in these specimens is also very similar to that of the type species, the shells appear to be considerably more inflated and the anterior adductor muscle scar is slightly smaller. These differences are confirmed by the new specimens described herein, in spite of the fact that none of them have a complete shell preserved. Yet, the internal molds in the new specimens, while missing the external ornamentation, show similar shell inflation to that of *M. argentinensis*, and are never as inflated as the molds of *M. mercerati*.

All known specimens of *M. pseudochorus* (Doello Jurado, 1922) are internal molds missing any trace of shell. However, these molds also show the large anterior adductor muscle scar and an outline and shape similar to those of the new specimens of the type species described herein. *Modiomytilus hauthali* (Ihering) from northwestern Chubut, exhibit a similar shell shape, although they appear to be slightly more elongate. The outer shell ornamentation is similar to that of the type species. Unfortunately, no interiors are well-enough preserved to show details of the muscle scars.

Biogeography: The geographic and stratigraphic ranges of the species included in *Modiomytilus* suggest that it originated in the Southern realm during the Paleogene, being restricted to shallow marine environments of Antarctica and along the Atlantic coast of Patagonia. The

earliest species of *Modiomytilus* appears to have been *Mytilosootus arcuatus* Stilwell and Zinsmeister, from the La Meseta Formation in Seymour Island (Antarctica). While incompletely preserved, the shells fit well in *Modiomytilus*. Very little is known about the Antarctic species as the internal molds have not preserved much of the internal shell features; however, they do show the unique large anterior adductor muscle scars. The La Meseta Formation was deposited during the late early Eocene (Stilwell and Zinsmeister, 1992), slightly earlier than the Río Turbio Formation, the age of which ranges from middle Eocene to early late Eocene (Malumián and Caramés, 1997). Mytilids in general have planktotrophic larvae and therefore show considerable dispersal potential. In addition, their byssate life habits also add to this capability, as they may raft across considerable distances attached —in the southern hemisphere— to kelp or driftwood (Fraser et al., 2010). Postlarval dispersal may be also possible by means of byssal threads (Sigurdsson et al., 1976; Baker, 1997). The Cenozoic fossil record in Antarctica is restricted to the Antarctic Peninsula and McMurdo Sound (GSA, Stilwell and Feldmann, 2000). It appears that Antarctic-South American dispersal likely took place during the early Cenozoic, as the Circum Antarctic Current had not been yet fully established, although surface water may have circulated to some extent in a West-East direction. This would have enabled the dispersal of other members of the Cenozoic faunas which are known to occur in high latitudes during the Paleogene, but appear in younger rocks in South America (Manceñido and Griffin, 1988; Beu et al., 1997; Casadío et al, 2010)

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Contribution to the biology and ecology of the spongivorous snail *Cerithiopsis greenii* (Gastropoda: Cerithiopsidae) in New England, USA

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ABSTRACT

Cerithiopsis greenii (C. B. Adams, 1839) is a common intertidal snail on rocky shores in southern New England in the summer and fall, and is also found in estuarine fouling communities. It feeds on the sponge *Halichondria bowerbanki* and in the laboratory also fed upon the sponge *Clathria prolifera*. *Halichondria bowerbanki* has expanded north of Cape Cod, Massachusetts, since the 1950s; we predict that, in concert with both warming trends and with prey expansion, *Cerithiopsis* has already moved, or will move, into northern New England.

Additional keywords: Cerithiopsis, spongivory, *Halichondria*, *Haliclona*, *Chalinula*, *Clathria*, climate change

INTRODUCTION

Many marine organisms, including invertebrates, fishes, and turtles, eat sponges either as specialized predators or opportunistic grazers (McClintoek et al., 2005; Peters et al., 2009; Todt et al., 2009). Marine snails, ranging from limpets and pleurotomariids to opisthobranchs, are especially well-known sponge predators (Strong and Harasweych, 1999; Beeerro et al., 2003; McDonald, 2007). Among shelled marine snails, speeies in the globally-oceurring hypsogastropod family Cerithiopsidae are widely-recognized as spongivores (for example, Fretter, 1951, and Marshall, 1978, who reviews aneedotal reeords from England, Alaska, California, Australia, and New Zealand), although actual observations of predation have been made for only a few species in the family.

Two species of *Cerithiopsis* occur along the New England coast of the United States (Emerson and Jaeobson, 1976; Rosenberg, 2009). The most common of these is *Cerithiopsis greenii* (occasionally misspelled *greenei* and often misspelled *greeni*), described in *Cerithium* by C. B. Adams in 1839 from Dartmouth harbor, Massachusetts, in Buzzards Bay, in southern New England. Adams (1839) noted that it was "found clinging to marine plants, a few feet below low water mark, in company with *Cerithium reticulatum*, Totten, and *Cerithium nigrocinctum*, Nob." The latter two species are now known as *Bittiolum alternatum* (Say, 1822) and *Marshallora nigrocincta* (C. B. Adams, 1839). Although Emerson and Jacobson (1976) stated that this speeies was named after Jacob Green, an American naturalist, this is in error; it was named for Thomas A. Greene of New Bedford, MA (Adams, 1839: 288), author of an often-overlooked early cheeklist of the marine shells of the state (Greene, 1833).

Cerithiopsis greenii is a small snail, the height of adult shells reported between 3 and 5 mm (Moore, 1961; Emerson and Jacobson, 1976; Andrews, 1981), although Pollock (1998) gave a size of 6 mm without noting a source. The shell of *Cerithiopsis greenii* is glossy-brown (amber glass) in color, with each post-nuclear whorl bearing three beaded spiral cords. The uppermost cord of each whorl, consisting of the smallest beads, may also form a black spiral band.

The published range of *C. greenii* is large, from the Gulf of St. Lawrence in Canada to Argentina (Bousfield, 1960; Farinati, 1994). However, as is typical of a number of marine invertebrates (Whiteaves, 1901), the Gulf of St. Lawrence populations (Winkley, 1888; Bousfield, 1960) are disjunet from the main populations of *C. greenii*, whieh are reported from southern Cape Cod and south (Table 1). Although historically recorded from the Gulf of Maine (Stimpson, 1851: Boston Harbor), it is not reported in modern times from northern New England (Wagner, 1979; Bromley, 1979; Trott, 2004, the latter summarizing historieal reeords rather than reeent surveys), leading us to suspect that the mid-nineteenth century Boston record may have been based upon specimens transported north, as discussed below. We comment below on its potential range north of Cape Cod.

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Table 1. Reported habitats of the spongivorous snail *Cerithiopsis greenii*, arranged geographically from north to south.

Location	Habitat	Reference
Canada: Gulf of St. Lawrence	in oyster beds, shallow water	Bousfield, 1960
Massachusetts: Boston Harbor	3 fathoms [5.5 meters]	Stimpson, 1851
Massachusetts: Dartmouth Harbor	"clinging to marine plants, a few feet below low-water mark", along with the snails *Bittiolum alternatum* and *Marshallora nigrocincta* [we interpret this as 3 to 4 feet, and thus 0.9 to 1.2 meters]	Adams, 1839
Massachusetts: Vineyard Sound	3 to 10 fathoms [5.5 to 18.3 meters] rocky shores; wharf piles; rocky bottoms of bays and sounds; in algae "on these bottoms" "gravelly and shelly bottoms"	Verrill and Smith, 1873
New York: Long Island	low water to 2 fathoms [4 meters]	Smith, 1859
New York: Long Island	dredged on oyster beds, along with the snails *Seila adamsii* and *Triphora* sp.	Balch, 1899
New York: Long Island	in eelgrass *Zostera marina* community, brackish water, 1-3 meters, "on silty sand bottoms, with low, slow tides"	Conrad, 1935
New York: New York City	in mud, sand, under stones and shells	Jacobson and Emerson, 1961
Delaware: Delaware Bay	mud-fine sand; estuarine in 28 – 32 $^{o}/_{oo}$	Leathem and Maurer, 1975
North Carolina: Newport River	on oyster beds	Wells, 1961
Florida: Indian River Lagoon	sea grass, mud, oyster beds, and sand	Mikkelsen et al., 1995
Mississippi: Ship Island	under side of rocks, on encrusting yellow sponge	Moore, 1961
Texas	bays, inlets, shelly sand; on marine plants	Andrews, 1981
Cuba	to 40 meters depth	Rolán and Espinosa, 1995
Mexico: Yucatan Peninsula	sand, marshes, rocky areas, and offshore reef	Vokes and Vokes, 1984
Mexico: central Gulf coast: Lobos Island and surrounding reef	among shell debris in sands near grass beds	Britton and Morton, 1989
Mexico: Tabasco	"epifaunal de aguas costeras y lagunares"	García-Cubas and Reguero, 1990
Costa Rica: Limon	under stones in seagrass *Thalassia* beds	Houbriek, 1968
Colombia	algae, gravel, and sand, in shallow estuarine water	Díaz-Merlano and Hegedus, 1994

Records of "*Cerithiopsis greenii*" in the southeastern United States and the Gulf of Mexico (Table 1, and Singley, 1893; Maury, 1922) include similar-looking sibling species (Rolán and Espinosa, 1995; Rolán et al., 2007, Lee, 2009). *Cerithiopsis greenii* sensu stricto may occur south to Florida (for example, Krisberg, 2009), but this requires confirmation (H.G. Lee, personal communication, September 2010). In more southern waters – Bermuda, the Caribbean, Cuba, Mexico, Costa Rica, Panama, Venezuela, and then south to Brazil, Uruguay, and Argentina, all of which are locations where *C. greenii* has been recorded (Verrill and Smith, 1873; Olsson and McGinty, 1958; Houbriek, 1968; Jensen and Clark, 1986; Figueiras and Broggi, 1988; Britton and Morton, 1989; García-Cubas and Reguero, 1990; Farinati, 1994; Rodríguez et al., 2003; Clavijo et al., 2005; Jensen and Pearse, 2009) – a similar species complex is involved (Rolán and Espinosa, 1995; Rolán et al., 2007). However, this species complex may not include the North American *C. greenii*. Molecular work may be required to resolve the distribution of the *C. greenii*-group in lower latitudes as well as in temperate South America.

Cerithiopsis greenii has been reported from a wide range of habitats. We summarize these in Table 1 (we include all records that we have found, including those in warmer waters that may well represent sibling species). Sponges are reported in only one case, but it is probable that sponges were either present and not recorded, were nearby, or the records represent dead shells. Rosenberg (2009) notes that while *C. greenii* is reported to 75 meters, living populations of *C. greenii* may occur only as deep as 15 meters. These small shells can drift both offshore and to shallower allochthonous habitats, and their planktotrophic larvae may be carried far afield as well (Jung [1975] and Thiriot-Quiévreux [1980] report larval shells from the Cariaco Basin off the north coast of eastern Venezuela, although, as noted above, records of *C. greenii* from this region may represent one or more other species). A number of authors have recorded this snail alive from both marine and estuarine (brackish) waters, as we do here.

While a meticulous work on the mollusks of the Long Island Sound region (Long Island Shell Club, 1988) reported *Cerithiopsis greenii* as "uncommon to rare" (based upon the occurrence of beach drift shells) and while we have found few modern-day records of this species in New England, we report here that it is a common intertidal snail in the summer and fall on the rocky shores of Rhode Island, and that it occurs in the Mystic River Estuary (Mystic, Connecticut) in vessel and other fouling communities. In the first report of its feeding

biology, we detail its predation upon the sponges *Halichondria bowerbanki* Burton, 1930 and *Clathria prolifera* (Ellis and Solander, 1786).

MATERIALS AND METHODS

Cerithiopsis greenii were collected from the edges of colonies of the yellow sponge *Halichondria bowerbanki*, in October and November 2008, from the underside of rocks in the low intertidal zone at Weekapaug Point, Westerly, Rhode Island. Also in November 2008, *C. greenii* were collected from a fouling community with yellow *Halichondria bowerbanki* on the hull of the CHARLES W. MORGAN at Mystic Seaport Museum in the Mystic River Estuary, Mystic; the MORGAN is an exhibit vessel and does not leave the estuary. Temperature and salinity data were collected at all stations.

In the laboratory, snails were maintained in 65 × 57 mm "tea ball" (tea strainer) plastic containers (mesh size 200 μm) in flowing aquaria at 12°C and 28–30‰. The snails were starved for 10 days prior to observational and experimental feeding studies.

Sponges for experimental use included *Halichondria bowerbanki* (yellow and green colonies) from intertidal rocks at Weekapaug Point and from Mystic River subtidal dockside fouling racks, *Chalinula loosanoffi* (Hartman, 1958) (= *Haliclona loosanoffi*), *Cliona* sp., *Clathria prolifera* (= *Microciona prolifera*), and *Halichondria bowerbanki* (orange colonies, which occur on the same racks with yellow colonies in the estuary). We used yellow, orange, and green (which contain zooxanthellae; Hartman, 1958) morphs of *Halichondria* to determine whether the apparent restriction of *C. greenii* to yellow *Halichondria* in the field was due to feeding preference or was a sampling artifact.

Sponges were kept in a temperature-controlled aerated incubator chamber at 5°C in 28–30‰ water for 24 hours before use. Sponges were identified using the diagnostic characters of Hartman (1958); sponge nomenclature follows that of the World Porifera Database (http://www.marinespecies.org/porifera/, accessed September 2010).

In the laboratory detailed observations of predation by *C. greeni* on sponges were made, and feeding was recorded through still and video photography, using a Motic Digital Microscope (DM 143, NTSC system) supported by Motic Images Plus software, Version 2.0. To observe feeding behavior, *C. greenii* were placed in 60 × 15 mm plastic Petri dishes in seawater at room temperature (21°C) with 2 mm^2 pieces of *H. bowerbanki* (yellow colonies from Weekapaug) for 3 to 4 days. The dish was later searched for fecal pellets that might further demonstrate prey consumption. Fecal pellets were examined under the compound microscope at 400× for the presence of spongin tissue and spicules.

Choice experiments similar to those performed by Becerro et al. (2003) were used to determine prey preference. Four snails (two from Weekapaug, and two from Mystic) were each offered 2 mm^2 pieces of six different sponge colonies, for a total of 4 controls and 20 treatments as follows: *H. bowerbanki* (Weekapaug, green colonies; yellow colonies from Weekapaug served as the control because *Cerithiopsis* is commonly associated with these in the field), *H. bowerbanki* (Mystic, orange colonies), *Chalinula loosanoffi*, *Cliona* sp., and *Clathria prolifera*. The snails were placed in separate 60 × 15 mm plastic Petri dishes with seawater; these trials were also conducted at room temperature (21° C). Observations were made for 10 minutes in order to establish if initial contact by a snail with the sponge would induce a feeding response (defined as proboscis moving and probing in a pumping fashion in order to scrape sponge tissue); if it did, snail behavior and prey consumption were recorded.

A separate experiment was conducted to examine potential predation given longer periods of prey availability. Twelve 2 mm^2 fragments of *Clathria prolifera* were placed in separate 60 × 15 mm Petri dishes filled with sea water and held at room temperature (21° C). A single snail was placed directly on top of each sponge fragment. Because *C. prolifera* tissue is red, we hypothesized that a snail which consumed the sponge tissue might produce red fecal pellets. At 24 and 48 hours the presence or absence, and color, of fecal pellets were recorded. At the end of the first 24 hour interval the few snails which had departed the sponge were placed back on the sponge fragments.

RESULTS

Our largest specimens of *Cerithiopsis greenii* from Weekapaug Point were 5.0 mm in height; our largest specimen from the Mystic River Estuary was 3.49 mm. The body is translucent-white, and, when extended across its sponge prey, can appear almost transparent against the spongin and spicules of *Halichondria*. A pedal gland on the posterior lobe of the foot produces mucus (Fretter, 1951), which then runs along the lobe's longitudinal furrow; the mucus assists the snail's locomotion (for example, we observed *Cerithiopsis* gliding on surface water tension in the laboratory), and may also play a role in securing the snail to its sponge prey, as noted by Fretter (1951) for *Cerithiopsis tubercularis* (Montagu, 1803) in England.

Habitat and Phenology: *Cerithiopsis greenii* was found in two habitats: the rocky intertidal of Rhode Island and subtidal fouling communities in Connecticut. At Weekapaug Point, Rhode Island, the snails were found under rocks in the low intertidal zone, alone or in pairs, exclusively associated with the yellow sponge *Halichondria bowerbanki*. Sponge colonies in October were commonly 10 cm in width, but by late November were 3 to 5 cm in width, with winter regression having commenced; concomitantly, snail abundance declined. In the Mystic River, Connecticut, other sponges occurring with yellow *Halichondria bowerbanki* include

orange-colored *H. bowerbanki*, *Chalinula loosanoffi*, *Clathria prolifera*, and *Cliona* sp. *Cerithiopsis greenii* was found only on yellow *Halichondria*.

Although the undersurfaces of rocks at Weekapaug Point are covered with an encrusting fauna, including the bryozoans *Schizoporella unicornis* Johnston, 1874 and *Cryptosula pallasiana* (Moll, 1803), the ascidians *Botrylloides violaceus* (Oka, 1927) and *Botryllus schlosseri* (Pallas, 1766), and the serpulid polychaetes *Hydroides dianthus* (A. E. Verrill, 1873) and *Circeis spirillum* (Linnaeus, 1758), no *C. greenii* were found associated with these other species. Other gastropods found near *C. greenii* under rocks included *Astyris lunata* (Say, 1826), *Costoanachis translirata* (Ravenel, 1861), *Costoanachis avara* (Say, 1822), *Lacuna vincta* (Montagu, 1803), and *Littorina littorea* (Linnaeus, 1758).

On the Rhode Island rocky shore temperatures ranged from 14.5° to 6°C in October and November 2008, and salinities were approximately 30‰. In the Mystic River in November 2008 snails were found in water of 10.9°C and a salinity of 26.9‰.

Feeding Biology We observed *Cerithiopsis greenii* feeding readily upon yellow *Halichondria bowerbanki* collected from both Rhode Island and Connecticut; unlike Fretter's (1951) report that she found *C. tubercularis* "reluctant to feed in captivity," such was not the case with *C. greenii*. Within minutes of initial contact with *H. bowerbanki*, *C. greenii* commenced feeding. In contrast, the other species of sponges presented to this snail elicited a distinctly different behavior: the anterior portion of the snail's foot would flail upon initial contact with non-*Halichondria* sponges, rapidly rising off the sponge, and no direct feeding was observed (but see below).

When feeding upon *H. bowerbanki* the extension of the snail's proboscis into the spongin was clearly visible (Figure 1). Feeding bouts during which *C. greenii* consumed sponge tissue lasted for up to 15 minutes, and occasionally somewhat longer. Proboscis movement alternated between rasping the spongin with a grating motion, and sucking loose tissue into the mouth with a strong pumping motion; tissue could be clearly seen entering through the proboscis. When viewed from above snails can appear to be almost motionless although feeding actively. Translucent yellow fecal pellets, approximately 200–300 µm in length, were found in the dishes with snails that were observed feeding. Pellets contained spongin only; no spicules were found therein.

Figure 1. *Cerithiopsis greenii* feeding on the sponge *Halichondria bowerbanki*. The snail's proboscis is extended into the sponge tissue.

After 24 hours in dishes with the red sponge *Clathria prolifera*, 3 (of 12 trial snails) had produced red fecal pellets, and after 48 hours, 7 (of 12) snails had produced red pellets, suggesting consumption of the red-colored spongin tissue of this sponge. In addition, one Mystic River snail was observed, in the 10-minute feeding bouts, to briefly consume green *H. bowerbanki* from Weekapaug.

DISCUSSION

We provide the first observations of the native Northwestern Atlantic snail *Cerithiopsis greenii* feeding upon the sponge *Halichondria bowerbanki*. While it has been proposed that *H. bowerbanki* is either introduced or cryptogenic in New England (Pederson et al., 2005; Connecticut Sea Grant 2010), the apparent feeding preference of *C. greenii* for this sponge, and its common association with *Halichondria* in the field, suggest that the sponge, too, may be native, in agreement with the conclusions of Vethaak et al. (1982).

Our observations that *Cerithiopsis* can also feed on the native sponge *Clathria prolifera* in the laboratory suggests, however, a potentially broader dietary range that may come into play when *Halichondria* is less available, or not available, as a food resource. In general, we observed predation in the laboratory only on yellow *Halichondria* and not on other color morphs, with a single exception of one snail that fed briefly on a green colony. More work needs to be undertaken relative to the presence of *C. greenii* in the field on the range of color morphologies of *Halichondria* (Hartman, 1958) and the ability of this snail to utilize non-yellow colonies.

The presence of *Cerithiopsis* in the Gulf of St. Lawrence since at least the 1880s (Winkley, 1888), well north of the known range of *Halichondria bowerbanki* at that time, suggests that some populations may rely on other prey species. *Halichondria panicea* occurs in the Gulf of St. Lawrence (Whiteaves, 1901), and may function as an alternative prey, although we note that this species also occurs in the Gulf of Maine (Hartman, 1958), where *Cerithiopsis* has not been reported (save for one 1850s Boston record, noted above and discussed below). Mitchell (1999) reports *Halichondria bowerbanki* from Northumberland Strait in the Gulf of St. Lawrence, based upon collections in the 1990s, and it is not impossible that it was historically present (as are a number of

otherwise-southern taxa in the southern Gulf of St. Lawrence, as noted earlier) but long overlooked.

Our observations are in agreement with those of Fretter (1951), who reported the European *Cerithiopsis tubercularis* feeding on the sponge *Hymeniacidon sanguinea* (Grant, 1826) [now known as *Hymeniaeidon perlevis* (Montagu, 1818)] in England, and of Collin (2004), who observed *Cerithiopsis gemmulosum* (C. B. Adams, 1850) feeding on the sponge *Haliehondria melanadocia* de Laubenfels, 1936 in Panama. Fretter and Graham (1962) later expanded the prey diversity of *C. tubercularis* to also include *Haliehondria* sp. and *Grantia* sp., and noted that another British species, *Cerithiopsis barleei* Jeffreys, 1867 fed on *Suberites domuncula* (Olivi, 1792). In the Northeastern Pacific, *Cerithiopsis stejnegeri* Dall, 1884 has been observed feeding on the edges of the sponge *Hymeniaeidon ungodon* de Laubenfels, 1932 in the rocky intertidal of Oregon (J. T. Carlton, unpublished). Through gut content analysis and direct observation of feeding, Fretter (1951) found that *C. tubercularis* used spongin for food and reviewed earlier observations that *C. tubercularis* deposited its eggs in sponge tissue, as does *C. gemmulosum* in Panama (Collin, 2004, who further demonstrated that snail larvae metamorphose when exposed to sponge tissue).

Haliehondria becomes dormant (degenerates) in the winter (Hartman, 1958; Fell et al., 1984), which our observations along the Rhode Island rocky shore further confirm. Where *Cerithiopsis* "over winters" is not known; they are absent from the undersurface of rocks along Connecticut and Rhode Island winter shores (J. T. Carlton, L. Haram, personal observations). It is possible that the snails embed themselves into the gravel-shell base underneath rocks in the intertidal, as does the snail *Littorina littorea*, which bury themselves along boulder edges in winter (J. T. Carlton, field observations). The discovery of *C. greenii* in a hull fouling community on the CHARLES W. MORGAN (albeit a stationary vessel) is reminiscent of Verrill and Smith's (1873) report of it from "wharf piles" (Table 1). That its occurrence in fouling communities is likely not uncommon is indicated by our finding it (2 January 1999) on *Haliehondria* on experimental fouling panels at Noank (mouth of Mystic River) and on *Haliehondria* in float (pontoon) fouling at a marina in the Mystic River (October 2010). We regard the few reports of it from fouling communities as representing under-sampling, or simply under-reporting, of small snails in this habitat [the record of *Cerithiopsis terebralis* by Hutchins (1952) from "buoy fouling" refers to another cerithiopsid now known as *Seila adamsii* (H. C. Lea, 1845)]. Its widespread occurrence on oyster beds (Table 1, Canada, New York, North Carolina, and perhaps Florida) suggests that there are a number of potential human-mediated dispersal vectors for this snail, including both vessel fouling and the movement of commercial oysters, and we suggest that the one-time report of *C. greenii* in Boston in the 1850s is likely due to transport by ships or oyster movements from southern waters.

Finally, we note that changing climatic conditions may potentially play a role in the distribution of *C. greenii*. Its host sponge, *Haliehondria bowerbanki* was not known north of Cape Cod prior to the 1950s (Sorte et al., 2010; J. T. Carlton, unpublished). *Haliehondria bowerbanki* spread north to the Bay of Fundy by the 1970s, in concert with a number of other southern taxa whose range expansions appear to be linked to warming coastal conditions (Sorte et al., 2010). We predict that, with both warming trends and with prey expansion, *Cerithiopsis greenii* may have already moved, or will move, into northern New England. In turn, in concert with predicted patterns of northward retreat of cooler-affinity taxa (Carlton, 2000; Sorte et al., 2010), the as yet uncertain southern border of *C. greenii* may be now shifting north as well.

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Albert R. Mead, 1915–2009, noted American malacologist: An obituary

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INTRODUCTION

The noted Ameriean malacologist Albert Raymond Mead (Figures 1–3) died in Tucson, Arizona, on 13 March 2009. An obituary is presented here by a foreign eolleague, friend and admirer, and Al Mead's son, in order to sketch a more eomplete picture beyond that published in various short obituary notices (e.g., Anonymous, 2009a–e; Bruggen, 2009; also in loeal newspapers).

Al, as he was affectionally known, was born on 17 July 1915 in San Jose, California. He earned his B.Sc. in entomology in 1938 at the University of California at Berkeley. From 1938 to 1940, Mead was at Cornell University (Ithaea, New York) where he was a Schaife Scholar and a John Henry Comstock Scholar in entomology. In 1940–1941, he was a graduate teaching assistant at the College of Agriculture at Davis (whieh, in 1959, became the University of California at Davis) and worked at the Marine Biological Laboratory, Woods Hole, Massachusetts. Returning to Cornell University, Mead earned his Ph.D. in 1942. While at Davis, he met a fellow student who beeame the love of his life, Eleanor Morrow; they married on 8 February 1942, a marriage that lasted 67 years until Al's death.

In 1942, Mead entered the U.S. Army as a 2nd Lieutenant in the Medieal Administration Corps and progressed to the rank of Captain. From 1943 to 1945, he was Parasitologist for the Western African Service Command (Inter-Allied Malaria Control Unit) in the Gold Coast (now Ghana, West Africa) where he was introduced to, and fascinated by, the study of the Achatinidae, the giant African snails. During his stay in Africa, Al befriended the Belgian scientist Dr. Joseph Charles Bequaert (1886–1982), who was working for the Belgian government as an entomologist. Following his work in Africa, Mead was transferred to the South Pacific theater of World War II where he continued his work on the pestiferous Giant African Snail (*Achatina fulica*). It was there that he met Dr. Yoshio Kondo (1910–1990), who later worked at the Bernice P. Bishop Museum, Honolulu, Hawaii, and was a life-long friend.

After an honorable diseharge from the U.S. Army at the end of World War II, Mead was awarded in 1946 a Postdoctoral Researeh Fellowship in Zoology at the University of California at Berkeley. In 1947, he subsequently obtained his life-long job as a Professor at the University of Arizona in Tueson. In 1952, he earned a Full Professor position and became Head of the Department of Zoology in 1956. He stepped down as department head in 1967. From 1967 to 1970, he was Chairman of the University of Arizona Marine Seienees Committee. From 1976 to 1980, Mead was the Associate Dean of the College of Liberal Arts. Upon retirement from the University of Arizona in 1985, Al beeame Professor Emeritus, having served almost 40 years. He was then able to devote all of his time to research of his scientifie passion, the giant African snails.

Mead served as the Ph.D. thesis ehair for a number of graduate students at the University of Arizona and also served on the thesis eommittees for other graduate students. Many of those developed into respeeted seientists, one even beeoming a faeulty eolleague of Mead at the University of Arizona (Walter Miller).

Al Mead was a clear proponent of professional soeieties and the dissemination of science. He was Chairman of the Pacific Division and National Vice President of the American Malacologieal Union in 1957, and President in 1963. In 1958, he became a Fellow and then President of the Southwestern and Rocky Mountain Division of the Ameriean Association for the Advancement of Seience, and by 1987 he was honored as an AAAS 50-year member. Mead was a Charter Member of the Arizona Academy of Scienee and its President in 1957. He was also a Charter Member of the Western Society of Malaeologists and the Soeiety of Invertebrate Pathology. Internationally he played a role in the Unitas Malacologica Europaea, later Unitas Malacologiea—the world

1

3

2

Figures 1–3. Albert R. Mead. **1, 2.** In action in West Africa, 2nd lieutenant US Army (1943–1945). **2.** As the world-renowned achatinid specialist at the University of Arizona (1990s).

body of malacologists. This institution organized the European Malacological Congresses, which evolved into the International Malacological Congresses. Al and Eleanor Mead always attended and Al never failed to lecture on his favorite achatinids, reason why many of his publications are abstracts of lectures at various meetings.

Although trained as an entomologist, Mead soon devoted his attention to the mollusks. Initially he was fascinated by the giant slugs of California (see his papers of 1942 and 1943 which derive from his Ph.D. dissertation; also 1960) but his professional career blossomed when he began researching the giant African snail in

Hawaii. Dr. Bequaert encouraged Mead to investigate the genitalia of the Achatinidae because he himself had met with difficulties in delimiting the giant African snail species on their shells alone. Indeed, the holdings of the family Achatinidae of most major museums usually were (and still are) limited to empty shells. Preliminary work by Henry A. Pilsbry (1862-1957) was the basis for Mead's 1950 work which established his fame as an achatinid specialist. In subsequent years he worked on the biology of the pest species *Achatina fulica*, publishing prolifically on this subject. His authoritative 1961 book became an instant best seller, and is now available on the Internet; an important update was published in 1979 in a multivolume book entitled "Pulmonates." He only returned to his beloved achatinid genital anatomy in the late seventies of last century; his 1979 paper was his first paper in that field after his 1950 anatomical treatise). His work in "economic malacology" (according to Alan Kabat, in litt., a term not first coined by Mead, cf. Bullen, 1905: 313) was published in the form of numerous short papers and reports in sometimes obscure and even ephemeral journals. At the same time, he also wrote a very widely distributed article for Reader's Digest (1949), with translations in several other languages. We have attempted to collate all publications and the list below (partly based on Mead's own notes) is as complete and as accurate as possible.

Always searching for material, Al traveled around the United States and later in western and central Europe, trying to trace old and new achatinid material, particularly type and preserved specimens. Some of these trips at that time were quite adventurous, even crossing the Iron Curtain into East Berlin (then in East Germany, D.D.R., a communist state). Al, the 'traveling snailsman' as he termed himself, always accompanied by Eleanor (who looked after accomodation and catering), made prolific notes and subsequently borrowed material to study and dissect at home. One of the important discoveries of those dissections was that the Madagasean genus *Leucotaenius* was not an achatinid, but rather belongs to the family Acavidae (1986). Thus, the Achatinidae are not indigenous to this island. The museums actively collecting achatinids (London, Tervuren, Leiden) were repeatedly visited and the senior author has fond memories of these sojourns. When in Leiden, the Meads always bedded down in a little local hotel not far from our (ACvB) house, Het Witte Huis (The White House) in Oegstgeest, the name of which appealed to Al's sense of humor.

The significance of Mead's research in the Achatinidae not only encompasses his detailed anatomical and systematic work, but also his recognition of the consequences of trying to control *Achatina* (and other non-native mollusks) when they were introduced into new regions. At times his views were controversial but his opinion was always based on the results of careful research. After Pilsbry, Mead was the first to study the genital anatomy of the achatinids from a phylogenetic point of view. The identity of the shells of the giant African snails is not always easily established and details of the genitalia are frequently required for conclusive species identification. Al Mead supplied these data and put them in context.

Al Mead was a successful taxonomist and in the course of his studies he introduced 11 new taxa in the mollusks and two in insects. These are enumerated below. Regarding eponyms, it is surprising that there are only two (which should be remedied in the near future!): *Archachatina (Tholachatina) meadi* Bequaert, 1950, Bulletin of Museum of Comparative Zoology 105 (1): 204 (Tanzania); *Sonorella meadi* Miller, 1966, The Nautilus 80: 50 (Arizona, USA) [anecdotal information supplied by Mead himself is that this species is characterized by a small penis!]. *Achatina eleanorae* Mead, 1995, was named by Mead after his spouse. Much of his data in the form of notes, drawings, etc., are still unpublished; these have been deposited in the archives of the National Museum of Natural History, Leiden, The Netherlands (now part of NCB/Naturalis—The National Centre for Biodiversity).

We appreciate the editorial suggestions from Alan Kabat (Washington, DC) and one anonymous reviewer for materially contributing to and considerably improving the manuscript by paying close attention to details.

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Bullen, R.A. 1905. Notes on land and fresh-water shells from the Alhambra Ditch, Granada, Andalucia, Spain; on Recent land shells from various localities near Carmona, Province of Sevilla; and on land, fresh-water, and marine shells from Holocene deposits, Carmona. Proceedings of the Malacological Society of London 6: 309–313.

LIST OF NEW MOLLUSK TAXA INTRODUCED BY A.R. MEAD

(all Gastropoda Pulmonata, one subfamily, three genera, six species, one subspecies)

Bequaertina, 1994, Bulletin of the Natural History Museum, London, Zoology 60 (1): 18, type species *Achatina graueri* Thiele, 1911 (East Central Africa from Zimbabwe to easternmost DR Congo and Uganda) (Achatinidae).

brachyphallus, *Ariolimax californicus*, 1943, American Midland Naturalist 30: 696 (holotype in California Academy of Sciences, San Francisco) (California) (Arionidae).

Bruggenina, 2004, Zoologische Mededelingen Leiden 78 (25): 443, type species *Archachatina sandgroundi* Bequaert, 1950 (Rift Valley from Zimbabwe to Rwanda and Tanzania) (Achatinidae).

Brownisca, 2004, Zoologische Mededelingen Leiden 78 (25): 445, type species *Archachatina neumanni* Thiele, 1933 (Sudan and Uganda to Somalia) (Achatinidae).

Callistoplepinae, 1994, Bulletin of the Natural History Museum, London, Zoology 60 (1): 18, type genus *Callistoplepa* Ancey, 1888 (Equatorial Guinea to western DR Congo) (Achatinidae).

dolichophallus, *Ariolimax*, 1943, American Midland Naturalist 30: 689 (holotype in California Academy of Sciences, San Francisco) (California) (Arionidae).

eleanorae, *Achatina (Lissachatina)*, 1995, Journal of Molluscan Studies 61: 265 (holotype in The Natural History Museum, London, U.K.) (East Africa, offshore islands of Tanzania) (Achatinidae).

kilburni, *Cochlitoma*, 2004, Zoologische Mededelingen Leiden 78 (25): 425 (holotype in Natal Museum, Pietermaritzburg, South Africa) (South Africa, Pondoland) (Achatinidae).

pilsbryi Mead and Miles, *Pallifera (Pancalyptus)*, 1960, The Nautilus 74: 75 (holotype in California Academy of Sciences, San Francisco) (Arizona) (Philomycidae).

puylaerti, *Archachatina (Calachatina)*, 1998, Journal of African Zoology 112: 125 (holotype in Zoologisches Museum Berlin, Germany) (Togo) (Achatinidae).

wigleyi, *Cochlitoma*, 2004, Zoologische Mededelingen Leiden 78 (25): 439 (holotype in Natal Museum, Pietermaritzburg, South Afriea) (South Africa, NE. of East London) (Achatinidae).

LIST OF NEW TAXA OF INSECTS INTRODUCED BY A.R. MEAD

(all Coleoptera Chrysomelidae, 2 subspecies)

magistrigata, 1938, *Donacia subtilis*, Pan-Paeific Entomologist 14 (3): 113 (holotype in California Academy of Sciences, San Francisco) (California).

occcidentalis, 1938, *Donacia distincta*, Pan-Pacific Entomologist 14 (3): 114 (holotype in California Academy of Sciences, San Francisco) (California).

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1938. New subspecies and notes on *Donacia* with key to the species of the Pacific States (Coleoptera, Chrysomelidae). Pan-Pacific Entomologist 14 (3): 113–120.

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Notice

Florida United Malacologists (FUM) 2012

The third meeting of Florida United Malacologists (FUM) will take place on Saturday, February 11, 2012, at The Bailey-Matthews Shell Museum (BMSM) on Sanibel Island, Florida. The one-day gathering is designed to enhance communication among professional, amateur, and student malacologists, with topics including, but not limited to biology, ecology, paleontology, archaeology, and conservation.

FUM follows the pattern established by similar informal gatherings such as BAM (Bay Area Malacologists), SCUM (Southern California United Malacologists), MAM (Mid-Atlantic Malacologists), and OVUM (Ohio (River) Valley United Malacologists). There is no formal membership and there are no dues, officers, nor publications. However, presenters are required to submit a brief abstract limited to 150 words or less. Abstracts will be posted on the Museum web site. The gathering will be free to presenters and Museum members. Non-members will be asked to donate the Museum admission fee of $9.

Participants are strongly encouraged to ask questions and discuss data, compare notes on methods and problems, and get acquainted with presenters and members of the audience. Presentations, limited to 15 minutes plus 5 minutes for questions, will be informal and will cover current research and collection efforts and issues. The Museum will provide projection equipment for PowerPoint programs, brief videos, and slides.

Due to staffing limitations, use of the library and research area and collection visits will be limited to two days prior to the gathering, Thursday, February 9, and Friday, February 10. Museum parking is free. Box lunches and dinner at a local restaurant (to be arranged) will be available at cost to participants and presenters. An event reservation form for presenters and participants will be posted soon on the Museum web site (www.shellmuseum.org). Seating is limited, so please return the reservation form prior to January 15, 2011.

Please send inquiries, reservations, and presentation topic submissions to José H. Leal, Museum Director/Curator at jleal@shellmuseum.org. The deadline for submission of topics and abstracts is January 31, 2011. The FUM program including abstracts, times, and sequence of presentations will be posted on the Museum web site, www.shellmuseum.org, shortly after the topic submission deadline.

Kind regards to all,

José H. Leal
Director/Curator
The Bailey-Matthews Shell Museum

THE NAUTILUS

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